United States
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**Agricultural
Research
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ARS-56

March 1987

# Biological Control of the Mediterranean Fruit Fly in the United States and Central America

ABSTRACT

Gilstrap, F.E., and W.G. Hart 1987. Biological Control of the Mediterranean Fruit Fly in the United States and Central America. U.S. Department of Agriculture, Agricultural Research Service ARS 56, 64 p.

This publication reviews the history of the most damaging species of the Old World tephritids, the Mediterranean fruit fly (Medfly), and the efforts to suppress this pest in the United States and Central America through biological control. The Medfly is a serious threat to agriculture throughout the world. The publication provides a historical perspective on the various expeditions that were undertaken to collect and establish parasites in Hawaii and Costa Rica. A section is included in the publication on interpretation of the results of these projects as a potential for more effective biological control of the Medfly in other countries of the Western Hemisphere.

KEYWORDS: Mediterranean fruit fly, Medfly, Ceratitis capitata (Wiedemann), Dacus dorsalis Hendel, oriental fruit fly, Dacus curcubitae Coquillett, melon fly, Neotropical fruit fly, tephritids

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By
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# BIOLOGICAL CONTROL OF THE MEDITERRANEAN FRUIT FLY IN THE UNITED STATES AND CENTRAL AMERICA

F.E. Gilstrap and W.G. Hart[1/]

## Introduction

Among the world's nearly 4,000 described species of fruit flies,[2/] only a relative few are serious pests of agriculture and these develop as larvae in commercial fruit or vegetables. Pest species occur in the genera Ceratitis Macleay, Pardalaspis Bezzi, Pterandrus Bezzi, and Dacus Fabricius of the Old World, and Anastrepha Schiner, Rhagoletis Loew, and Toxotrypana Gerstaecker of the New World. The most damaging Old World tephritids to invade the New World are Ceratitis capitata (Wiedemann) (Mediterranean fruit fly or Medfly), Dacus dorsalis Hendel (oriental fruit fly), and Dacus cucurbitae Coquillett (melon fly). Though occasional infestations of D. dorsalis have occurred on the U.S. mainland, each has been quickly eradicated and both D. dorsalis and D. cucurbitae in the New World remain confined to Hawaii. A fourth Old World species, Dacus tryoni Chilean possession in the Pacific Ocean, in 1972 and again in 1974 but was eradicated on each occasion (Autter 1977, Bateman 1973).

In addition to the three established species of Old World fruit fly pests, at least 71 genera and 818 species of indigenous neotropical fruit flies are known in the New World (Foote 1967, 1980). Rhagoletis species, as revised and discussed by Bush (1966), are frequently of concern to agriculture in the Nearctic Region but tend to be less important than Anastrepha, Toxotrypana, or Ceratitis species in the Neotropical and southernmost Nearctic Regions. This is particularly true when considering international plant quarantine regulations. Several Neotropical fruit fly species attack important commercial crops in parts of United States. These species are Anastrepha fraterculus (Wiedemann), A. ludens (Loew) (Mexican fruit fly), A. obliqua (Macquart) (= A. mombinpraeoptans Sein) (West Indian fruit fly), A. suspensa (Loew) (Caribbean fruit fly), and Toxotrypana curvicauda Gerstaecker (Papaya fruit fly) (Stone 1942). Each listed Anastrepha species reportedly includes Texas and/or Florida as part of its northernmost distribution (Foote 1967; Stone et al. 1965) and at least three cause concern for commercial agriculture. T.

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2/Diptera: Tephritidae (= Trypetidae, Trypaneidae, and Trupaneidae).

curvicauda, which infests papaya, has been collected in both Texas and Florida (Benjamin 1934); A. ludens occasionally attacks citrus produced in the Texas Rio Grande Valley (Stone 1942); and since 1965, A. suspensa has been a resident of at least 30 counties in southern Florida where it infests citrus and other species of tropical and subtropical fruit (Baranowski and Swanson 1971).

A History of Medfly

The present distributions of melon fly and oriental fruit fly are relatively restricted and include much of southeast Asia, India, Pakistan, Hawaii, and for melon fly, parts of Africa (Anonymous 1956, 1960). Medfly, in contrast, is distributed over much of Africa and presently occurs on each major continent (Anonymous 1951). Medfly damage to commercial crops is frequently documented in early entomological literature, placing Medfly in the Azores, Madeira Island, and the Cape Verde Islands by 1829 (Macleay 1829); Spain by 1842 (Breme 1842); Algeria by 1858 (Villenueve as recorded by Quaintance, 1912); Italy by 1863 (Rondani 1870); Bermuda by 1865 (Back 1914); Tunis (= Tunisia), Mauritius, People's Republic of Zaire (= Belgian Congo, Congo, or Kongo), and the Cape Coast of the Republic of South Africa (= Union of South Africa) by 1885 (Roder 1885); Australia by 1897 (Fuller 1897); Turkey, Spain, and Brazil by ca. 1900 (Compere 1910); France by 1906 (Girard 1906); Uganda and Egypt by 1910 (Froggatt 1910); Hawaii by 1910 (Silvestri 1914); and the Federal Republic of Nigeria, Ghana (= Gold Coast), Benin (= Dahomey), Delagoa (part of Mozambique), New Zealand, and Argentina by 1912 (Silvestri 1914).

Since the earliest reports of damage, Medfly has spread to include at least parts of most countries in Africa, the Mediterranean basin, and South and Central America. Specific countries hosting Medfly are listed by the Commonwealth Agricultural Bureaux (Anonymous 1951), Gutierrez-S. (1976), and Mitchell et al. (1977). In South America, Medfly has been reported from Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, Uruguay, and Venezuela (Mitchell et al. 1977). According to Gutierrez-S. (1976), Medfly also occurs in Columbia, Guyana, Surinam, French Guyana, and Ecuador. Thus, Medfly has been reported from at least parts of every mainland country in South America. Medfly was first discovered in Central America in 1955. The original Medfly discoveries were on the highland plateau of Costa Rica near the towns of Santa Ana and Hatillo (on the outskirts of San Jose) (Morales-M. 1963, Rhode 1976). Medfly has since extended its range to El Salvador, Honduras, Guatemala, Nicaragua, and Panama, though it apparently has not yet invaded Belize (Mitchell et al.

1977). Most recently, Medfly invaded Chiapas, Mexico, in 1977 (Anonymous 1978). Thus, Medfly in the Western Hemisphere presently resides in most of South America, Central America, southern Mexico, and Hawaii.

Messenger and Flitters (1954) suggested that Medfly in the continental United States could not sustain itself as a continuously viable population north of 30° north latitude. Medfly invaded Florida in 1929, 1956, 1962, 1963, and 1981; Texas in 1966; and Los Angeles County, California, in 1975 (Cunningham et al. 1980, Rhode 1976) and 1980 (Hagen et al. 1981). Each U.S. infestation except for those in California was south of 30° north latitude, each was in an environmentally favorable area as described by Messenger and Flitters, and all were eradicated. However, an infestation of Medfly discovered on June 5, 1980, in Santa Clara County in the San Francisco Bay area of California, was north of even the 35° north parallel. This is distinctly outside areas considered favorable for Medfly survival by Messenger and Flitters. The infestation, the object of an intensive eradication effort (Hagen et al. 1981), was declared eradicated in September 1982. Baas (1959) reported that Medfly in Germany, Switzerland, and France, occurred continuously during the mid-1950's in the "...same orchards and gardens..., and survives the winter in these countries... as a pupa or at times also in the imaginal stage." Medfly's northernmost European distribution as described by Baas (1959) is 50°north latitude, and all the continental United States lies south of that parallel.

From the foregoing, it is evident that Medfly could probably reside as a permanent resident in several Southern States, and conceivably could reside in several northerly States. In fact, the Medfly infestation of Santa Clara County, which almost certainly survived the 1980 winter, is distinct and inauspicious evidence of Medfly's capacity to persist in areas not included in Messenger's and Flitters' predictions. Additionally, Medfly has an extremely wide host range which exceeds 200 species and varieties of fruits and vegetables (Mitchell et al. 1977; Weems 1981), and many of these hosts are commonly produced in the continental United States. Risk of Medfly establishing permanently in relatively large contiguous areas on the U.S. mainland is substantial, considering its wide distribution in the Western Hemisphere, apparent tolerance to relatively wide extremes of temperature, wide host range, and the rapid and frequent movement of people and commerce between infested and uninfested areas.

Originally described in 1824 by Wiedemann as Trypeta capitata from specimens reportedly from the East Indies (Quaintance 1912), C. capitata received initial notice following Macleay's (1829) report of C. citriperda Macleay (= C. capitata according to Roder, 1885) being "very destructive to orange." Froggatt (1899) first applied the term 'Mediterranean fruit fly' to this species as he believed Medfly originated in the Mediterranean region. However, numerous scientists have since placed Medfly's aboriginal home as somewhere in tropical Africa. The Italian dipterist M. Bezzi (according to Silvestri, 1914) considered Medfly's aboriginal home to be in the tropical lowlands of West Africa; whereas, Van Zwaluwenburg (1937) suggested Medfly probably originated "... in the mountainous forests of equatorial or east Africa." According to Silvestri (1914), the natural habitat of C. capitata "... is certainly tropical Africa south of 8° north latitude ... but I do not think one can affirm whether it be the whole of that region or only the western part until accurate studies have been made." Though an origin of East versus West Africa is still not known, Silvestri (1914), Bezzi (in Silvestri, 1914), Back and Pemberton (1918), Quayle (1938), N. L. H. Krauss (personal communication), and H. K. Munro (1964) all agree on an origin in equatorial Africa. According to Munro (personal communication), the great diversity of Ceratitinae in tropical Africa is strong support for that contention.

## Collecting and Establishing Parasites of Medfly

Biological control of Medfly has been used with varying levels of success in Australia, Italy, Brazil, Costa Rica, Nicaragua, Bermuda, the Republic of South Africa, Spain, Algeria, Egypt, Israel, the Canary Islands, Mauritius, Morocco, and Hawaii (Clausen 1978). However, most of these programs were essentially redistributions of known parasites from other importation programs, usually Hawaii. In fact, Hawaii importation programs are the only ones of major significance, both in terms of numbers of parasite species imported and in the impact of parasites established. Thus, this review is confined to the Hawaiian and associated fruit fly biological control programs in the Western Hemisphere.

Medfly biological control in Hawaii is the result of three projects wherein parasites were sought explicitly for Medfly, one project seeking biological control of the melon fly and one seeking biological control of the Oriental fruit fly. Of the two non-Medfly parasite projects in Hawaii, only the Oriental fruit fly project resulted in fortuitous but important added control of Medfly. Costa Rica was the object of the only other major parasite importation program conducted against Medfly in the Western Hemisphere. These

six projects and the parasites and their origins are reviewed below in the following sections.

The Mediterranean fruit fly was discovered in Honolulu, Hawaii, in 1910, apparently accidentally introduced with fruit brought by steamship from Australia (Back and Pemberton 1918; Silvestri 1914). Because the Italian entomologist F. Silvestri had expressed a previous interest and was experienced with fruit flies and their natural enemies (Fullaway 1915), he was funded in 1912 by the Hawaii Board of Agriculture and Forestry to search for natural enemies of Medfly. Silvestri left Italy in July 1912, and traveled by steamer to Africa, visiting the Canary Islands, Senegal, Guinea (= French Guinea), the Federal Republic of Nigeria, the United Republic of Cameroon (= Kamerun), Ghana (= Gold Coast), Benin (= Dahomey), the People's Republic of Zaire (= French and Belgian Congo), Angola, the Republic of South Africa (= Union of South Africa), and Australia (table 1).

Silvestri collected 16 species of parasites from 18 species of fruit flies including 10 species of Ceratitinae (table 1). Despite Silvestri's numerous collections from equatorial West Africa, he reared only 4 Medfly individuals and collected only two adults. However, Silvestri was cautiously optimistic regarding the relatively few Medflies collected. He acknowledged that Medfly rarity in tropical Africa may have been due to the brevity of his collecting, but he also felt a possibility that C. capitata was held in check by important inimical factors. Though he did not discover any parasites of Medfly per se, he suggested that the fruit fly parasites attacking other fruit fly species, including parasites he collected, were at least partially responsible for the rarity of C. capitata. He also suggested that intensive study of Medfly in Nigeria and Benin would contribute substantially towards an explanation for the rarity of the Medfly in equatorial West Africa.

Because of the rigors and duration of travel, Silvestri lost most of his parasite cultures before arrival in Honolulu. He did transport, however, cultures of five species: 300 individuals of Coptera (as Galesus) silvestrii (Kieffer) (Diapriidae), 500 of Dirhinus giffardii Silvestri (Chalcididae), 5 of Opius humilis Silvestri (Braconidae), 12 of O. perproximus Silvestri, and 7 of Biosteres (as Diachasma) tryoni (Cameron) (Braconidae). Between June 1 and September 30, 1913, the Hawaii project released 11,590 individuals of C. silvestrii, 8,035 of D. giffardii, 16 females of B. tryoni, and 3 females of O. humilis (Fullaway 1914). The fifth species, O. perproximus, was not released

(Fullaway 1914). These releases resulted in establishing only the pupal parasite, D. giffardii, and the two larval-pupal parasites, B. tryoni and O. humilis. The few braconid individuals released were the only such parasites released during the original establishment efforts (Fullaway 1915).

However, 1,657 additional individuals of O. humilis were later redistributed from field collections during October 1 through December 31, 1913 (Bridwell 1914).

The 1914 Hawaiian Medfly Parasite Project

Silvestri's 1912-13 collections in Africa revealed numerous species of fruit fly parasites which had promise but were not successfully transported to Hawaii. Thus, the Hawaii Board of Agriculture and Forestry funded D.T. Fullaway and J.C. Bridwell to conduct a second collecting trip for Medfly parasites. Fullaway and Bridwell arrived in Lagos, Nigeria, in July 1914 and collected for ca. 3 weeks at Olokemeji, ca. 100 miles inland from Lagos (Fullaway 1915). During this time they initiated cultures of Tetrastichus giffardianus Silvestri (Eulophidae) [as reported by Silvestri (1915) and not T. giffardii Silvestri as reported by Fullaway (1915)], Biosteres (as Diachasma) fullawayi (Silvestri) (Braconidae), an Opius sp. (Braconidae), and a Spalangia sp. (Pteromalidae) (Fullaway 1915, Back and Pemberton 1918). Fullaway left Nigeria on August 19, 1914, transporting cultures of the four parasite species to Hawaii and leaving Bridwell behind at Olokemeji to collect for three more months. Fullaway was unable to maintain cultures of the two undescribed parasite species he transported to Hawaii but did culture and release 18,050 individuals of T. giffardianus and 195 of B. fullawayi during 1914 (Fullaway 1915). Bridwell ultimately left Nigeria with a quantity of parasitized material, which included a fifth parasite species, Biosteres (as Hedylus) desideratus (Bridwell). However, he became seriously ill while enroute and during his recuperation in South Africa and Australia eventually lost all parasite cultures (Fullaway 1915). Thus, only T. giffardianus and B. fullawayi were released and definitely established in Hawaii as a result of the 1914 Fullaway-Bridwell collections.

Fullaway also introduced a species of dung-fly parasite, Pachycrepoideus vindemmiae (Rondani) (as P. dubius Ashmead) and Spalangia philippinensis Fullaway (= S. endius Walker), to Hawaii from the Philippine Islands during 1914 for control of dung-breeding flies. The former species was recovered in small numbers from C. capitata pupae during 1915 and 1916 (Back and Pemberton 1918; Pemberton and

Willard 1918a). However, S. philippinensis is not mentioned in subsequent literature until 1961 (Bess et al. 1961).

The 1935-36 Hawaiian Medfly Parasite Project

The third Medfly parasite collecting effort was made in 1935-36, when collectors were sent to West Africa, East Africa, Brazil, Malaysia (= Malaya), Sri Lanka (= Ceylon), and India (Bianchi and Krauss 1936). The 1935-36 project was sponsored by the U.S. Department of Agriculture and was administered by C. P. Clausen, Chief of the Division of Foreign Parasite Introduction, Washington D.C. Initial funding for the project was derived from the Sugar Processing Tax which was abolished in January 1936, when the Agricultural Adjustment Administration was declared unconstitutional. Regular USDA funds of the Bureau of Entomology and Plant Quarantine were eventually allocated after the program began, but they were insufficient to complete foreign collections as originally planned. Thus, the 1935-36 project was prematurely terminated (Clausen 1956), and though many parasite species were collected in Africa and southeast Asia (tables 2-4), most did not survive transport to Hawaii.

Collecting in West Africa by R. H. Van Zwaluwenburg and J. H. McGough took place from November 1935 to July 1936. They traveled to Sierra Leone, Liberia, Ivory Coast, Ghana (= Gold Coast), the Federal Republic of Nigeria, the United Republic of Cameroon (= French Cameroons), Angola, and the People's Republic of Zaire (= Belgian Congo) (table 2) (Van Zwaluwenburg 1936). Van Zwaluwenburg (1936) reported that most fruit suitable for Medfly development in West Africa are available during December-March. He also reported that, in his opinion, the most promising region for parasite collection Yaounde, Cameroon, where fruit was most available during May-June. Van Zwaluwenburg, like Silvestri before him, observed that C. capitata was quite rare in West Africa. Neither he nor McGough reared a single specimen from collected fruit, though they did observe museum specimens of C. capitata reared from citrus in Ghana. Van Zwaluwenburg (1936) suggested the preferred host of C. capitata would probably be "...some obscure and little known native fruit...in a rain forest or savannah country at a fairly high elevation...similar to that of Yaounde in the French Cameroons...." According to Van Zwaluwenburg's records (1936, 1937), at least 18 species of tephritids were collected during his and McGough's travels, of which 9 were Ceratitinae, and at least 5 species of tephritid parasites were collected (table 2). Only three of these five parasite species were successfully transported to Hawaii and these were Opius perproximus (Braconidae), Biosteres (as Hedylus) giffardii (Silvestri) (Braconidae), and Biosteres

caudatus Szepligeti. Each of the three species was released; however, none apparently became established (Clausen et al. 1965; Clausen 1978).

F.A. Bianchi and N.L.H. Krauss worked in East Africa from November 1935, to June 1936 collecting in the United Republic of Tanzania (= Tanganyika), the Island Sultanate of Zanzibar (now part of Tanzania), Kenya, and Uganda (Bianchi and Krauss 1936, 1937). They obtained at least 14 species of tephritids, 7 of which were Ceratitinae, and at least 13 species of tephritid parasites (table 3). Their work, however, was fraught with serious handicaps due to the primitive region in which they were working and funding problems. Bianchi and Krauss made a four shipments of parasites, the first three of which were delayed enroute causing all parasites to emerge and die before transshipment from Paris to New York. Parasite material in these three shipments had been obtained mostly from Sersalisia usumbarensis at Amani, Tanzania. The fourth shipment was carried personally by Bianchi and Krauss on their return voyage to the United States, but again all parasites emerged and died enroute. Thus, Bianchi and Krauss did not ship any living parasites to Hawaii. Bianchi and Krauss recommended that in order for future Medfly parasite collections to be particularly productive in East Africa, collections should include the Busingiro Forest and the Nile Province of Uganda (in September-December) and the Nairobi and highland areas of Kenya (in July- September).

D. T. Fullaway conducted the Brazilian portion of the 1935-36 program, collecting there from October 1935 to April 1936 (Fullaway 1936). Fullaway's collecting was much less productive in numbers of fruit fly species collected than other portions of the 1935-36 program. According to Fullaway (1936), the purpose of collecting in Brazil was to obtain parasites of indigenous fruit flies which might be fortuitously well-adapted to Medfly. Interest in South America as a source of Medfly natural enemies stemmed from accounts by George Compere who reported collecting numerous parasites and predators of fruit flies in Brazil in 1904 (Compere 1912). Fullaway's Brazilian tephritid collections were comprised primarily of Anastrepha fraterculus and A. serpentina, both indigenous to the Neotropical region, and of C. capitata, which was exotic. Most of Fullaway's fruit fly parasite collections consisted of two species, Doryctobracon areolatus (Szepligeti) (as Opius cereus Gahan) (Braconidae) and Opius bellus Gahan (Fullaway 1936). Only Opius bellus Gahan was released in Hawaii and apparently did not become established (Clausen 1978).

F.C. Hadden collected from December 1935 to June 1936 in Malaysia (= Malaya), Sri Lanka (= Ceylon), and India (Hadden 1936). Hadden obtained six species of fruit flies and seven species of fruit fly parasites (table 4). The only Medflies he reported observing occurred in Sri Lanka where the fly was not yet established but often present in shipments of fruit from other parts of the world. None of the parasites shipped by Hadden became established in Hawaii (Clausen 1978; Corbett 1937).

Though not a part of the 1935-36 Hawaiian Medfly parasite project, Aceratoneuromyia (as Syntomosphyrum indicum) indica (Silvestri) (= Melittobia indicum Silvestri) (Eulophidae) was introduced to Hawaii from India in 1938 (Bess et al. 1961, Noble 1942). No reports of recovery were noted until that of Clausen (1956), which followed its release for a second time during the 1947-52 Oriental fruit fly parasite importation program.

In summary, the 3 Hawaiian projects addressed specifically to importation of Medfly parasites searched in 17 African countries and Australia, Malaysia, India, Sri Lanka, and Brazil and collected 15 species of Ceratitinae, namely Bistrispinaria fortis (Speiser), Carpophthoromyia tritea (Walker), Ceratitis capitata, Pardalaspis antistictica (Bezzi), P. bremii (Guerin-Meneville), P. cosyra (Walker), P. giffardi (Bezzi), P. punctata (Wiedemann), P. silvestrii (Bezzi), Pterandrus anonae (Graham), P. colae (Silvestri), P. rubivorus (Coquillett), Trirhithrum nigerrima (Bezzi), T. coffeae Bezzi, and T. nigrum (Graham). All species listed except C. capitata are known only from the Ethiopian region. Also, these projects resulted in establishment of five fruit fly parasites in Hawaii; namely, Dirhinus giffardii, B. fullawayi, O. humilis, B. tryoni and T. giffardianus. Except for B. tryoni, each established parasite species was obtained in Africa from a species of Ceratitinae.

## The 1915-16 Hawaiian Melon-Fly Parasite Project

The melon fly, D. cucurbitae, was first reported in the Hawaiian Islands by D.W. Coquillett (1899) following collections there by G. Compere in 1898 (Back and Pemberton 1917; Compere 1912). However, melon fly had apparently been accidentally introduced to Hawaii from Japan years before Coquillett's report (Back and Pemberton 1914, 1917). Melon fly attacks more than 60 species of vegetables and fruits. It prefers primarily Cucurbitaceae as hosts, though it also attacks legumes, tomatoes, oranges, figs, peaches, mangos, and papayas among others (McBride and Tanada 1949). In 1915, D.T. Fullaway was engaged by the Hawaii Board of Agriculture and Forestry to obtain natural enemies of melon fly from its aboriginal home in the Indo-Malayan region

(Back and Pemberton 1917, Clausen 1978). In 1915, Fullaway traveled to Singapore of Malaysia (= Malaya), collecting there during August-October; Java (of the Dutch East Indies or Indonesia) during October-November; India during November-December; and the Philippine Islands during January-April of 1916 (Fullaway 1920). Fullaway obtained Opius fletcheri (Braconidae) Silvestri from Java and India, and a Spalangia sp. (Pteromalidae) from Java only. However, he transported only O. fletcheri to Hawaii where it was first released in 1916 and was verified as established in 1917 (Pemberton and Willard 1918a).

Though other parasites imported to attack Medfly and Oriental fruit fly also occasionally attack melon fly, the levels of such parasitism are generally quite low (Pemberton and Willard 1918a, Nishida and Haramoto 1953). In fact, Pemberton and Willard (1918a) conducted intensive studies on the interaction of melon fly hosts, Medfly parasites, and O. fletcheri. Where only larval Medfly parasites occurred within melon fly larvae, the melon fly larvae always encapsulated the parasite larva(e) and matured to adult melon flies. However, O. fletcheri larvae always overcame the melon fly host's resistance "... by toxic substances injected into the (host) larva by the female of O. fletcheri ..." during oviposition. The only Medfly parasite capable of maturing on melon fly was T. giffardianus, and this only when the host larva already contained an O. fletcheri larva which ensured destruction of the host's natural resistance to parasite development. Consequently, T. giffardianus could develop on D. cucurbitae only at the expense of O. fletcheri. On the other hand, O. fletcheri apparently rarely attacks Medfly larvae in the field (Willard 1920a). Thus, the 1915-16 melon fly biological control project in Hawaii apparently contributed very little to biological control of Medfly and the 1912-14 Medfly parasite introductions contributed almost nothing to melon fly control.

## The Hawaiian Oriental Fruit Fly Biological Control Project

The next major effort at biological control of a fruit fly in Hawaii was in 1947-51 for the oriental fruit fly, Dacus dorsalis. The oriental fruit fly was first discovered in Hawaii on May 10, 1946, and apparently had been present undetected for some time (Carter 1950). Efforts to import exotic natural enemies of D. dorsalis were initiated by the Hawaii Board of Agriculture and Forestry in early 1947. These efforts were joined in a cooperative venture in mid-1948 by the U.S. Department of Agriculture (Bureau of Entomology and Quarantine), Hawaii Agricultural Experiment Station, Hawaiian Sugar Planters Association Experiment Station, and the Pineapple Research Institute (Carter 1950).

Parasite collections were made during 1947-51 by one or several cooperators in China (= People's Republic of China), Formosa (= Nationalist China or Taiwan), North Borneo, Malaysia (= Malaya), Australia, Java, New Britain, Saipan, New Caledonia, Fiji, Sri Lanka (= Ceylon), India, Philippine Islands, Thailand, Republic of South Africa (= Union of South Africa), People's Republic of Zaire (= Belgian Congo), Mozambique, United Republic of Tanzania (= Tanganyika), Kenya, Uganda, Central African Republic (= French Equatorial Africa), Cameroon, Zambia (= North Rhodesia), Zimbabwe (= South Rhodesia or Rhodesia), Brazil and Mexico (Clancy et al. 1952; Clausen 1956, and Clausen et al. 1965).

The University of California joined the Hawaii foreign collecting effort in 1949, conducting explorations during 1949-51 for parasites in Taiwan and southern China and conducting studies for mass culture of parasites in Hawaii (Carter 1950; Clancy et al. 1952). The total program resulted in 64 species and varieties of parasites (table 5) being imported to Hawaii for control of D. dorsalis. Of the 64 species and varieties, 26 attacked Medfly in laboratory studies, 28 were released, 14 were subsequently recovered, and 8 new species or varieties reported established (Clausen et al. 1965). According to laboratory studies reported by Clausen et al. (1965), each of the eight species or varieties established also attacked Medfly. These are Opius fletcheri Silvestri, O. incisi Silvestri, Biosteres (as Opius) longicaudatus var. malaiensis (Fullaway), B. l. var. novocalendonicus (Fullaway), B. l. var. taiensis (Fullaway), B. (as Opius) oophilus (Fullaway), B. (as Opius) persulcatus Silvestri [= B. vandenboschi (Fullaway)] (all Braconidae), and Aceratoneuromyia indica (Silvestri) (as A. indicum) (Eulophidae).

During the 1947-52 importation program five parasite species were recovered from pupae considered to be Medfly and originating in Africa, namely Bracon celer Szepligeti (Braconidae), Opius africanus Szepligeti (Braconidae), O. humilis, Tetrastichus dacicida Silvestri (Eulophidae), and T. giffardianus. O. humilis and T. giffardianus had already been established during the 1912-13 and 1914 Medfly parasite importation-release programs; however, neither B. celer nor O. africanus were released during the Oriental fruit fly biological control project. T. dacicida was colonized with other Tetrastichus spp. (Clausen et al. 1965) but apparently did not establish as evidenced by their absence in studies of Bess et al. (1961) and Haramoto and Bess (1970).

According to Clausen et al. (1965), the three parasites which ultimately proved most important for control of D. dorsalis (i.e., B. longicaudatus var. malaiensis, B. vandenboschi, and B. oophilus) were imported during the earliest importation efforts by the Hawaii Board of Agriculture and Forestry in 1947-48 and before the Board was joined by the other cooperators. Furthermore, these parasites were collected from the Philippine Islands and Malaysia, the area thought to be the aboriginal home of D. dorsalis, and each was easily established in Hawaii. Thus, parasites which provided most control of D. dorsalis were collected very early in the program from an area expected to possess the best parasites and these established quickly exerting significant control. However, Clausen et al. (1965) proposed that future searches for exotic natural enemies of fruit flies should not be confined exclusively to the host's aboriginal home as both B. tryoni, from D. tryoni in Australia (Silvestri 1914), and B. oophilus, from D. dorsalis in Malaysia and India (Bess 1953), have at times provided significant control of C. capitata in Hawaii.

Costa Rican Medfly Parasite Projects

After the Hawaii parasite importation project on D. dorsalis was concluded in 1953, no major importation projects were initiated in North America to obtain new parasites from outside the Western Hemisphere. However, a major parasite redistribution project was initiated in Costa Rica shortly after Medfly's discovery there in 1955. This program was chronicled by E. Morales-M. (1963) in an unpublished report. According to Morales-M., the Costa Rican program was sponsored by agreements between the Costa Rican Ministry of Agriculture, the Organismo Internacional Regional de Sanidad Agropecuaria (OIRSA), the Servicio Tecnico Interamericano de Cooperacion Agricola (STICA), the Mexican Ministry of Agriculture, and the U.S. Department of Agriculture. The Costa Rican program began as an importation project in 1955, shifting to an augmentation project in 1958.

During the 1955-56 importation phase, parasite species released were Biosteres (as Opius) longicaudatus var. novocalendonicus, B. l. var. taiensis, B.(as Opius) vandenboschi, B. (as Opius) oophilus, B. (as Opius) tryoni, and O. incisi (all Braconidae); Dirhinus giffardii (Chalcididae); Aceratoneuromyia indica (as Syntomosphyrum indicum) (Eulophidae); and Trybliographa daci Weld (Cynipidae). All individuals (total = 28,348) of each listed species originated in Hawaii and on arrival in Costa Rica were released directly in several locations. Recoveries of released parasites included A. indica, B. longicaudatus, B. oophilus, and T. daci (Morales-M. 1963). Because only 1 individual of B. oophilus was recovered, and

this in 1956, little hope was held that it had become established. No field recoveries were reported for B. vandenboschi, B. tryoni, O. incisi, or D. giffardii.

Parasites from laboratory cultures in Mexico and/or Hawaii were released in Costa Rica by the OIRSA/STICA during 1958-62 to augment natural populations of already released and established Medfly parasites. Species released in 1958-59 were A. indica, B. longicaudatus, B. vandenboschi, B. oophilus, D. giffardii, and B. tryoni, and in 1960-62 were A. indica and B. longicaudatus. An overwhelming majority of the 540,000 parasites released during 1958-62 were either A. indica (ca. 65%) or B. longicaudatus (ca. 25%) (Morales-M. 1963). During 1963-82, the OIRSA/Costa Rica Ministerio de Agricultura y Ganaderia (CRMAG) continued the augmentative release of parasites, and maintained cultures of released parasites in San Jose, Costa Rica. The OIRSA/CRMAG releases during 1963-82 included the following species: A. indica, B. longicaudatus, Opius concolor Szepligeti, D. giffardii, and P. vindemmiae (Gonzales-A. 1963, 1966, 1972, 1981). The O. concolor culture was obtained in 1966 from the Institute National de la Recherche Agronomique in France, and that of P. vindemmiae from the Commonwealth Institute of Biological Control (CIBC) in India/Pakistan via the CIBC in Trinidad (Gonzales-A. 1966).

Cultures of the other released species were obtained from the USDA in Hawaii. A shipment of B. tryoni was also obtained in 1966 from the USDA, in Hawaii, but could not be cultured and thus was not released (Gonzales-A. 1966). Cultures and releases of D. giffardii were terminated in 1972 because of production costs and its apparent lack of efficacy (Gonzales-A. 1972). The OIRSA/CRMAG program of 1963-82 has been essentially an extension of the previous 1958-62 augmentation program, though the species of parasites released varied some from year to year. During the 1963-82 culturing, several of the named parasites species were shipped for release in Guatemala, El Salvador, Panama, and Nicaragua (Mitchell et al. 1977; Gonzales-A., personal communication).

Today, we are concerned of the Medfly spreading from Central America to Mexico and the probability of its moving ultimately through Mexico to the continental United States. Thus, a cooperative research project on biological control of Medfly in Costa Rica was initiated in August 1978 by F.E. Gilstrap and W.G. Hart. This program consists of agreements between the Costa Rican Ministry of Agriculture, OIRSA, USDA-ARS Subtropical Crop Insects Research Unit at Weslaco, TX, and the Texas Agricultural Experiment Station at College

Station. Gilstrap and Hart began the program in 1979 with a 2-year survey of extant indigenous and exotic parasite species attacking fruit flies in Costa Rica. Initial surveys (Wharton et al. 1981) affirmed establishment of B. longicaudatus and A. indica over much of Costa Rica and also documented establishment of B. oophilus. Data were not obtained on the pupal parasites, D. giffardii and P. vindemmiae.

The Gilstrap-Hart Costa Rican project re-introduced B. tryoni to Costa Rica during the summer of 1981. B. tryoni was field collected in Hawaii in cooperation with T.T.Y. Wong of the USDA-ARS, Tropical Fruit and Vegetable Research Laboratory in Honolulu, and shipped to the OIRSA laboratory where a culture was initiated. Results from releases of B. tryoni are not yet available.

The ultimate objective of the current Costa Rican Medfly project is to obtain previously collected (as summarized in tables 1-3) and perhaps new species of fruit fly parasites from Africa for introduction to Costa Rica. Such collections are scheduled for December 1981 through December 1982 with release and evaluation to take place during 1982-83.

## Impact of Parasites on Medfly

### Medfly Biological Control in Hawaii During 1913-46

Biological control of Medfly during 1913-47 consisted mostly of parasitism by four species of parasites established from Silvestri's 1912-13 and Fullaway- Bridwell's 1914 importations, i.e., the three solitary braconid, larval-pupal parasites, Opius humilis, Biosteres tryoni, and B. fullawayi; and the gregarious, eulophid larval-pupal parasite, Tetrastichus giffardianus. The two pupal parasites imported and released were easily mass reared (Fullaway 1914), though the diapriid, Coptera silvestrii, apparently did not become established (Pemberton and Willard 1918a) and the chalcidid, D. giffardii, has been credited with contributing very little to Medfly control (Willard and Mason 1937). The braconids, on the other hand, were much more difficult to rear (Bridwell 1916) and were released in relatively small numbers (Fullaway 1914; Back and Pemberton 1916); but they established easily and rapidly caused substantial suppression of Medfly (Back and Pemberton 1916). The following reviews Medfly control by these parasites prior to the 1947 Oriental fruit fly parasite importation program.

Medfly parasite recoveries began in October 1913, about 6 months after initial releases of Silvestri's four species of fruit fly parasites (Fullaway 1915). During the first 6

months of 1914, parasitism of Medfly was due mostly to O. humilis with extremely low levels of parasitism reported for B. tryoni (Back and Pemberton 1915), and there were no published reports for recoveries of D. giffardii. By late 1915, four species of parasites were routinely recovered: O. humilis, B. tryoni, B. fullawayi, and T. giffardianus, and each was apparently well established (Back and Pemberton 1916). However, data from coffee collected during July-December 1915 indicated a shift in relative abundance of parasite species as parasitism by B. tryoni was greater than that of O. humilis in most samples (Back and Pemberton 1916). This shift in parasite balance continued during 1916 (Pemberton and Willard 1918b) and 1917 (Pemberton and Willard 1918c), with the shift also becoming clearly evident on most other host fruit.

Parasitism by O. humilis dropped from an annual average of 17.2% in 1916 to 12.7% in 1917, and B. tryoni, B. fullawayi, and T. giffardianus each gained in parasitism, from 13.3 to 20.3%, 2.1 to 7.3%, and 0.6 to 7.2%, respectively. The shift towards B. tryoni dominance was not expected, probably in part because B. tryoni was obtained from an Australian tephritid only distantly related to Medfly; whereas the other introduced parasites came at least from the same part of the world as Medfly and from more closely related hosts. Average total parasitism for all parasite species increased during this period, gaining from 33.2% in 1916 to 47.5% in 1917.

Pemberton and Willard (1918a) initiated studies in 1916 on biologies, interrelationships, and efficacy of the introduced Medfly parasites. Their report described the four common parasites plus two previously unrecorded parasites of Medfly, i.e., the larval-pupal parasite, Opius fletcheri, introduced in 1916 for control of melon fly (Fullaway 1920), and Pachycrepoideus vindemmiae (as P. dubius), the pupal parasite introduced in 1914 for control of dung flies (Back and Pemberton 1918, Pemberton and Willard 1918a). Both of these species were characterized as occasional Medfly parasites of very minor importance. Pemberton and Willard described in detail the morphology and biology of immature stages, and behavior and biology of adults for each of the four common parasite species. All four species attacked medium to mature larvae, but according to Back and Pemberton (1916), O. humilis, B. tryoni, and B. fullawayi preferred host fruit still attached to the tree. Adults of T. giffardianus, however, frequently oviposited in fallen fruits and were even collected as adults searching for hosts inside fruits on the ground. Back and Pemberton (1916) speculated that such behavior in T. giffardianus

should eventually enhance its suppressive value. Pemberton and Willard (1918a, 1918c) reaffirmed from their 1916-17 work that O. humilis excelled during cooler months of the year and at cooler sampling locations.

In February 1918, Pemberton and Willard (1918d) published an ominous note stating their concern for continued increasing parasitism by B. tryoni, B. fullawayi, and T. giffardianus, at the expense of parasitism by O. humilis. Their intensive field and laboratory studies in 1916-17 showed that larval B. tryoni, B. fullawayi, and T. giffardianus almost invariably killed larvae of O. humilis when any of the former occurred in the same Medfly host with the latter. They also found that T. giffardianus usually survived any opiine if present together in the same Medfly host. They concluded that mortality of parasites caused by other parasites reduced total parasitism and overall Medfly control and that such mortality was particularly detrimental to O. humilis which their early field and laboratory studies indicated had the most desirable attributes for efficient Medfly control (see also Back and Pemberton 1918). The ultimate inference to be made from Pemberton and Willard's paper is that O. humilis possibly should have been the only parasite species introduced and that future biological control importation projects should ascertain in advance the best parasite for release to avoid the parasite shifts and "interference" as occurred in Hawaii.

An excellent rebuttal to Pemberton and Willard's concerns was published by H.S. Smith (1929). Smith asserted that Medfly control was improved by the collective action of all parasites even when O. humilis was not dominant. Smith's arguments are extremely important for continued biological control efforts against Medfly, other fruit flies, and for biological control as a scientific discipline. Actually, better evidence may exist for questioning the value of T. giffardianus because of the genuine, though apparently negligible, interference of T. giffardianus with control of D. cucurbitae by O. fletcheri (see previous section on "The 1915-16 Hawaiian Melon Fly Parasite Project"). However, further studies are needed before condemning T. giffardianus. These studies should (1) elucidate the magnitude of interference in melon fly biological control, and (2) determine the propensity of T. giffardianus to preferentially oviposit in previously parasitized melon fly or Medfly immature stages. Such studies would separate simple intrinsic superiority (sensu Smith 1929), a trait which would be either of positive or neutral value for fruit fly control, and true hyperparasitism which would definitely be negative and undesirable.

Trends of parasitism for 1918-24 continued to be basically true as reported for 1914-17 (Willard 1920b, 1923; Willard and Bissell 1926, 1930). Total annual parasitism by O. humilis declined from a high of 31.5% in 1915 to a low of 4.1% in 1923, with a 1914-24 10-year average of 12.3%. B. tryoni parasitism ranged from a low of 0.3% in 1915 to a high of 34.6% in 1918, had a 10-year average of 20.4%, and after 1916 invariably caused the greatest average annual parasitism in most types of fruit. B. fullawayi parasitism remained fairly constant with a 10-year average of 4.8%. T. giffardianus parasitism fluctuated widely from a low of 0.6% in 1916 to a high of 25.3% in 1923, with a 10-year average of 8.1%. Total parasitism during 1914-24 ranged from a low of 33.2% in 1916 to a high of 56.4% in 1921, and a 10-year average of 45.6%.

Willard and Mason (1937) undertook a 20-year review, from 1914 to 1933, of Medfly parasitization. By 1937, a rather clear understanding was possible for causes of differences in parasite efficacy in different fruit, especially because the adjustments in balance between parasite species had essentially stabilized. As early as 1916, Pemberton and Willard (1918b) had noted certain physical properties of fruit as important for successful parasitism, which were confirmed with the 20-year review (Willard and Mason 1937). Soft, thin- skinned fruit with relatively shallow pulp and large seeds (e.g., coffee or Indian almond) had consistently higher levels of parasitism; whereas, fruit with thick or tough-textured skin or deep pulp (e.g., guava, citrus, mango, or West Indian medlar), or both characteristics, generally had much lower levels of parasitism. Braconid parasitism was greatest where Medfly larvae were close to the fruit exterior and where fruit skin was easily penetrated by the parasite's ovipositor.

Willard and Mason (1937) reported that relatively large collections of coffee cherries during 1923-33 usually produced barely enough Medfly larve to record parasitism and that parasitism which did occur generally measured in excess of 90%. However, Willard and Mason also commented that such levels of parasitism were not general for all fruit or all locations and that the Kona coffee district was the only area where Medfly was under good biological control. O. humilis was the dominant parasite species in coffee from 1914-17, but was superseded by B. tryoni during 1918-22. Between 1922 and 1929, B. fullawayi caused greater Medfly parasitism in coffee than O. humilis and B. tryoni combined, but after 1929, B. tryoni again dominated and O. humilis became either extremely rare or was eliminated

completely from Kona coffee (Willard and Mason 1937, Clausen et al. 1965).

Annual rates of Medfly parasitism from all host fruit collected from all Medfly infested areas after 1914 ranged from 24.9 to 55.8%, with an average annual rate of 42.3% for the 20-year period. However, Medfly continued as a serious pest (Willard and Mason 1937). To minimize losses, commercial producers adopted the practice of picking fruit in the earliest stages of maturity, thus usually suffering little or no Medfly infestation (Willard and Bissell 1926). Willard and Bissell noted that records reported for Medfly parasitism in edible host fruits (e.g., mango, peaches, and persimmons) were usually obtained from ripe, well-infested fruits and not from fruits normally destined for commercial markets.

No further studies of Medfly parasitism in Hawaii were published between the Willard and Mason report of 1937 and the introduction of new parasites to control oriental fruit fly in 1947.

Medfly Biological Control in Hawaii After 1946

Discovery of the oriental fruit fly in Hawaii in mid-1946 prompted a major fruit fly parasite importation program (see previous section on "The Hawaiian Oriental Fruit Fly Biological Control Project"), with the first new parasites being released in March 1947 (Carter 1950; Clausen et al. 1965). According to Clausen et al. (1965), the total number of released natural enemies eventually exceeded 3.25 million individuals and included at least 28 species and varieties. (Note: Bess et al. (1961) counted 4 species established in previous programs and thus reported 32 species released.) Extensive laboratory studies led to decisions preventing release of potential secondary parasites (e.g., several of the pupal parasites studied by Dresner (1954)), and also revealed each primary parasite species' capacity to develop on laboratory cultures of Oriental, melon, and/or Mediterranean fruit fly (Clausen et al. 1965). Clausen's studies (1965) disclosed numerous parasite species, including every new species eventually established, as capable of parasitizing Medfly. These results were early indicators of improved Medfly biological control which was hoped would accrue as an added benefit from the Oriental fruit fly project.

Studies to ascertain parasite establishment began soon after inital releases, but because larvae and pupae of C. capitata and D. dorsalis could not be reliably separated, field parasitism for each parasite species per fly species could only be estimated (i.e., only host pupal remains are

available for fly identification when pupae produce parasite adults). Until Yamada et al. (1962) developed a key for separating pupae, the procedure in each sample was to record respective numbers of emerged adult flies and parasites and then infer the relative numbers of each fly species parasitized by each species of emerged parasite. Consequently, accurate specific host-parasite records were not reported.

By 1951, eight new species of parasites were established (table 5), and each could parasitize Medfly at least under laboratory conditions. However, only three of the eight species (i.e., B. longicaudatus, B. vandenboshi, and B. oophilus) eventually caused significant control of either D. dorsalis or C. capitata. Of the 24 species of parasites collected in Africa during 1948-51 (Clausen et al. 1965), only Tetrastichus giffardianus, T. dacicida Silvestri, Opius phaeostigma Wilkinson, Biosteres (as Opius) bevisi Brues, 2,000 individuals of unidentifiable Opius spp., and Dirhinus giffardii were released (table 5) (Bess et al. 1961, Clausen et al. 1965). Both T. giffardianus and D. giffardii had already been established in Hawaii during the 1912-14 Medfly projects, and no individuals of O. phaeostigma, O. bevisi, or Opius spp. were reported as recovered. According to Bess et al. (1961), T. dacicida was the only new exotic African parasite released which was subsequently recovered (in collections during 1948-53), and according to Clausen et al. (1965) neither T. dacicida nor any other new African parasite species was established. Thus, no new parasites were established from the aboriginal home of Medfly during the 1947-51 parasite importation program in Hawaii.

Field studies of fruit fly natural enemies commenced soon after the first parasites were released. The most consistent collection records for both D. dorsalis and C. capitata were obtained from guava, a widely distributed and suitable host for both flies in Hawaii. Bess (1953) was one of the first researchers to study Medfly dynamics in Hawaii after the Oriental fruit fly established. According to Bess, the D. dorsalis invasion in 1946 caused a rapid, nonparasite induced decline in Medfly populations infesting guavas, peaches, and other fruits, and this decline was especially evident in guavas at lower elevations. But, larvae of neither C. capitata nor D. dorsalis caused reductions in numbers of adults of the other when larvae of both occurred in the same fruit (Bess 1953). Bess' data and discussion do not provide a definitive explanation for the apparently precipitous decline of C. capitata, and only suggested that interspecific competition between the two fly species was somehow responsible. The second phenomenon reported by Bess (1953) was that though both fly species

occurred throughout Hawaii, D. dorsalis was numerically dominant in tropical lowlands and C. capitata in the more temperate uplands and that C. capitata was numerically dominant at elevations of 500 to 1,000 feet during late winter and spring and D. dorsalis during the fall. Bess stated that both phenomena were unrelated to parasite activity, which at the same time was also having a distinct suppressive effect on both fly species.

Several changes in parasite species dominance occurred soon after the new oriental fruit fly parasites were established. These changes which were similar to those previously described for Medfly parasites during 1914-33. According to Bess et al. (1950) and van den Bosch et al. (1951), both B. longicaudatus and B. vandenboschi readily established on the islands of Oahu, Hawaii, Maui, and Kauai. B. longicaudatus remained most numerous until October 1949, when it was superseded by B. vandenboschi on Oahu. During the summer of 1950, B. oophilus, initially unrecognized as a distinct species (van den Bosch and Haramoto 1951), replaced B. vandenboschi as the dominant parasite on Oahu and has remained dominant to the present. Eventually, this same sequence of parasite dominance was repeated throughout the larger islands of Hawaii.

According to van den Bosch and Haramoto (1953), the early dominance of B. longicaudatus was probably due to the large numbers of insectary-produced individuals (ca. 104,000 (Bess et al. 1950)) released during 1948-49. As these releases became fewer and smaller, the advantage was lost. The natural potential for increase of B. vandenboschi, coupled with its habit of attacking 1st instar host larvae and its usually successful competition when larvae of both parasite species occur in the same host, permitted B. vandenboschi to attain dominance. The ultimate and overwhelming dominance of B. oophilus after 1950 was due largely to its ability to attack host eggs and to its almost always preventing development of eggs of its parasitic competitors (i.e., B. longicaudatus or B. vandenboschi, B. oophilus) (van den Bosch and Haramoto 1953).

The addition of new parasite species during 1947-51 also caused a shift in balance of previously established Medfly parasites (Bess et al. 1961; Haramoto and Bess 1970). B. tryoni and B. fullawayi were readily recovered from Medfly infested coffee and peaches up until about 1950 (Bess et al. 1961), after which time they became relatively scarce, as did O. humilis in 1933. Parasitism of fruit flies in coffee after 1951 was reported by Haramoto and Bess (1970) as follows: B. tryoni, B. fullawayi, B. longicaudatus, B.

formosanus Fullaway, B. compensans (Silvestri), O. incisi, and Aceratoneuromyia indica were each measured at less than 1% of the total parasitism; parasitism by B. vandenboschi at ca. 6%; and parasitism by B. oophilus generally greater than 90%. According to Clausen et al. (1965), O. humilis completely disappeared on Oahu by the late 1930's but remained present in the Kona area of the Island of Hawaii. However, Haramoto and Bess (1970) did not recover O. humilis from Kona coffee during their 1966-68 parasite sampling program. They stated that it had not been seen or reared since 1950. Thus, it may also have been displaced from the Island of Hawaii, though further studies are necessary to establish this as fact.

A gradual increase in parasitism of C. capitata and D. dorsalis occurred in coffee at Kona during 1949-53 (Bess et al. 1961) and apparently occurred at all elevations (Bess 1953). These same trends also occurred in guava on the islands of Hawaii, Maui, and Molokai during 1950-52 and on Oahu during 1949-53 (Bess et al. 1961). According to Bess et al. (1961), B. oophilus accounted for more than 90% of all D. dorsalis parasitism during mid-1951 to early 1954 in guavas, averaging ca. 70% parasitism. Parasitism of C. capitata was much greater than before introductions of new parasites.

Newell and Haramoto (1968) conducted an intensive study of various sources of mortality affecting D. dorsalis during 1949-54. Their studies revealed that excessive intraspecific competition among D. dorsalis larvae in 1948 had substantially diminished by 1949 and that D. dorsalis was definitely being suppressed by parasites during 1949. Newell and Haramoto calculated that by 1951-52, the D. dorsalis population was only ca. 6% of its epidemic peak in 1948, and thereafter was only ca. 7-8% of the previous maximum. Considering only D. dorsalis as a host, they determined that ca. 95% of the eggs laid by D. dorsalis during 1951-52 were parasitized, and that ca. 80% of these died before hatching. The prehatch mortality was explained as due to trauma from multiple oviposition by several to many B. oophilus or to microbial infection of host eggs after B. oophilus oviposition. They concluded that this host egg mortality probably had a negative effect on the ability of B. oophilus to suppress fruit flies, as each such host egg killed was also a killed potential adult of B. oophilus. However, they also concluded that regardless of such mortality B. oophilus continued to effect significant suppression of D. dorsalis populations. Though Newell and Haramoto did not include C. capitata in their studies of host egg mortality, B. oophilus does attack Medfly. Thus,

it seems reasonable at present to assume that the Newell-Haramoto statistics on prehatch mortality may also apply to Medfly.

Following the Medfly parasitism studies by Bess (1953) and Bess et al. (1961), the next study of fruit fly parasitism which deals explicitly with Medfly was not until the work of Haramoto and Bess (1970) in 1966-68. According to Haramoto and Bess, the numbers of D. dorsalis larvae per 300 coffee cherries declined from 42.4 in 1949 to less than 5.0 after 1951 and of C. capitata from 22.1 to less than 10.0 after 1952. At the same time, total average parasitism increased from 8.7 in 1949 to greater than 50% (range 51.1 to 76.6%) during 1951-68. They concluded that populations of both flies in guava and coffee were much lower during 1966-68 than before 1950 (or essentially the same as during 1952-56), and that parasitism of both flies had averaged 65-70% in infested fruits of both plants since 1952. They also concluded that most such parasitism in both fly species was due largely to B. oophilus. Thus, biological control of Medfly apparently was substantially improved, at least in some fruit types, as a result of the 1947-51 parasite establishments for the oriental fruit fly.

## Summary and Interpretation

As a result of Hawaii's continued efforts at fruit fly biological control during 1912-51, a reported 26 parasite species were released. Of these, only Biosteres bevisi, B. caudatus, B. giffardii, B. fullawayi, Coptera silvestrii, Dirhinus giffardii, Opius humilis, O. perproximus, O. phaeostigma, Tetrastichus giffardianus, T. dacicida, and Trybliographa daci originated from the continent of Africa. Also as a result of the 1912-53 fruit fly parasite importations, the following 14 parasite species were reportedly established in Hawaii: Aceratoneuromyia indica, B. fullawayi, B. longicaudatus, B. oophilus, B. tryoni, B. vandenboschi, D. giffardii, O. fletcheri, O. humilis, O. incisi, B. kraussii, Pachycrepoideus vindemmiae, Spalangia endius, and T. giffardianus. Regarding the 14 parasite species established, the following facts are of particular note: (1) Only O. humilis, B. fullawayi, D. giffardii, and T. giffardianus originated from the continent of Africa; (2) only O. humilis was obtained from Medfly per se, but not from its probable aboriginal home in tropical Africa, (3) only B. fullawayi, D. giffardii, and T. giffardianus were obtained from tropical Africa; but not from Medfly per se, and (4) only B. oophilus, B. tryoni, and O. humilis were regarded as important for Medfly control over an extended period in Hawaii.

The Mediterranean fruit fly continues to threaten permanent establishment on the U.S. mainland coming from either Hawaii and/or Central or South America. The 1980-82 Santa Clara County infestation is evidence of Medfly's capacity for survival in areas previously considered by some researchers to be outside its potential distribution in North America. The earlier mainland infestations in California, Texas, and Florida are evidence of its ability to invade by commerce or private travel, or both. Agriculture in the United States should re-evaluate attitudes toward geographic or climatic immunity to Medfly depredation and redouble efforts to minimize risk of its successful invasion. Two such efforts should be (1) implementation of a plan to eradicate Medfly from Hawaii and (2) improved biological control of Medfly not just in Costa Rica but also in other Medfly-infested countries of the Western Hemisphere. The effect of the first mentioned is obvious, and the effects of the last are threefold. First, the inoculative reservoir of Medfly from which an accidental U.S. mainland introduction could originate would be reduced; second, other species of fruit flies such as Anastrepha spp., Rhagoletis spp., or Toxotrypana spp. might be significantly suppressed and thus benefit the host countries; and third, new exotic parasites established in Western Hemisphere countries could function

as an immediate source of Medfly parasites should Medfly establish on the mainland of the United States.

The usual worldwide Medfly control tactic in commercial crops is regular application of pesticide/bait combinations. However, Hawaii has obtained substantial control and benefit from releases of exotic fruit fly parasites. The magnitude of dooryard fruit infestations is less in Hawaii because of the parasite activity which causes reduced Medfly population pressures. This permits local use of fruit not protected by pesticides. Benefits of Medfly biological control to Hawaii's commercial fruit producers are similar to those for dooryard fruit, but are less well recognized and merit better documentation. Regardless, the number of Medflies which can emigrate to commercial orchards from nearby wild host or dooryard fruit is substantially less than in the absence of parasites, thus making any preharvest protections from infestation more effective and needed less often.

The control of Medfly with parasites in Hawaii, even though not complete, is indicative of a potential for at least similar levels of Medfly biological control in other Western Hemisphere countries. As listed in tables 1-5, numerous species of fruit fly parasites have not yet been introduced or established, or both, in the Western Hemisphere, and for many, aside from funding for importation and release, the primary obstacles to their release for establishment are only the tests for freedom from hyperparasite habit.

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Table 1.
Summary of fruit flies and parasites[1] collected by F. Silvestri in Africa and Australia during July 1912 to May 1913 (extracted from Silvestri 1914)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2] |
|---|---|---|---|---|
| Canary Islands | VII-30. | Ceratitis capitata (Wiedemann) | peaches | - |
| Senegal | VIII-2 & VIII-3. | Ceratitis giffardi Bezzi | Chrysobalanus sp. | Diachasma fullawayi Silvestri. |
| | | Certitis silvestrii Bezzi | Chrysobalanus sp. | - |
| | | Dacus longistylus Wiedemann | Calotropis procera | Opius dexter Silvestri. |
| French Guinea | VIII-4 to VIII-31 & X-5 to XI-6. | Certatitis giffardi Bezzi | Sarcocephalus esculentus | Biosteres caudatus Szepligeti. |
| | | Ceratitis punctata (Wiedemann) | Plumieria longiflora | Diachasma fullawayi Silvestri.<br>Galesus silvestrii Kieffer.<br>Hedylus giffardii Silvestri. |
| | | Dacus armatus Fabricius | cucumbers<br>melons | - |
| | | Dacus vertebratus Bezzi | - | - |
| Nigeria | XI-7 to XII-29. | Ceratitis anonae Graham | Aberia caffra (?)<br>Anona sp. | Biosteres caudatus Szepligeti.<br>Dirhinus giffardii Silvestri.<br>Galesus silvestrii Kieffer.<br>Spalangia afra Silvestri. |
| | | Ceratitis capitata (Wiedemann) adults | Eugenia uniflora | - |
| | | Ceratitis giffardi Bezzi | Sarcocephalus esculentus | Biosteres caudatus Szepligeti.<br>Tetrastichus giffardii Silvestri.<br>Diachasina fullawayi Silvestri. |
| | | Ceratitis nigerrima Bezzi | unknown drupe<br>coffee | - |

Table 1. Continued
Summary of fruit flies and parasites[1] collected by F. Silvestri in Africa and Australia during July 1912 to May 1913 (extracted from Silvestri 1914)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2/] |
|---|---|---|---|---|
| Nigeria (Con.) | | Ceratitis stictica var. antistictica Bezzi | Oxyanthus sulcatus | Biosteres caudatus Szepligeti.<br>Tetrastichus giffardii Silvestri. |
| | | Ceratitis tritea (Walker) | Pyrenacantha vogeliana | Biosteres caudatus Szepligeti.<br>Diachasma fullawayi Silvestri.<br>Opius inconsuetus Silvestri.<br>Tetrastichus oxyurus Silvestri. |
| | | - | Sarcocephalus esculentus | Dirhinus ehrhorni Silvestri. |
| Kamerun | XII-30 to I-9. | Ceratitis colae Silvestri | Cola acuminata | - |
| | | Ceratitis nigerrima Bezzi | Eugenia uniflora | Biosteres caudatus Szepligeti. |
| | | Ceratitis punctata (Wiedemann) | papaya<br>Theobroma cacao | - |
| | | Dacus bipartitus Graham | Momordica sp. | Biosteres caudatus Szepligeti.<br>Diachasma fullawayi Silvestri.<br>Tetrastichus giffardii Silvestri. |
| | | Trypaneid larva | ? | Opius inquirendus Silvestri. |
| Gold Coast | I-13 to I-29. | Ceratitis colae Silvestri | Cola acuminata | Tetrastichus giffardii Silvestri. |
| | | Ceratitis nigerrima Bezzi | coffee | Galesus silvestrii Kieffer.<br>Opius perproximus Silvestri. |
| Dahomey | I-31 to II-10. | Ceratitis capitata (Wiedemann) | Chrysobalanus ellipticus | - |
| | | Ceratitis giffardi Bezzi | Chrysobalanus ellipticus | Galesus silvestrii Kieffer.<br>Opius perproximus Silvestri.<br>Tetrastichus giffardii Silvestri. |

| | | | | |
|---|---|---|---|---|
| | | Dacus brevistylus Bezzi | Momordica sp. | Biosteres caudatus Szepligeti.<br>Opius perproximus Silvestri. |
| Congo | II-12 to II-20. | - | - | - |
| Angola | II-21 to II-28. | - | - | - |
| South Africa | III-6 to III-26. | Ceratitis capitata (Wiedemann) | peaches<br>pears<br>quince | Dirhinus sp.<br>Galesus silvestrii Kieffer.<br>Opius humilis Silvestri.<br>Opius perproximus Silvestri.<br>Trichopria capensis Kieffer. |
| | | Ceratitis rubivora Coquillett | Rubus sp. | - |
| | | Dacus brevistylus Bezzi | watermelon | - |
| | | Dacus lounsburyi Coquillett | watermelon<br>cucumber | - |
| | | Dacus oleae Gmelin | Olea verrucosa | Bracon celer Szepligeti. |
| Australia | IV-16 to IV-26. | Dacus tryoni (Froggatt) | Schizomeria ovata | Diachasma tryoni (Cameron). |

1/ Scientific names listed are those used by reporting scientist and may not be the most current or accepted binomials available.
2/ Listed parasites may not have been recovered from all listed host fruit.

Table 2.
Summary of fruit flies and parasites[1] collected by R.H. Van Zwaluwenburg and J.M. McGough in West Africa during November 1935 to July 1936 (extracted from Van Zwaluwenburg 1936)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2/] |
|---|---|---|---|---|
| Sierra Leone | XI-9 to IV-4. | Ceratitis anonae Graham | Anisophyllea laurina | Opius sp. |
| | | Ceratitis giffardi Bezzi | Sarcocephalus esculentus | Biosteres caudatus Szepligeti.<br>Opius perproximus Silvestri.<br>Tetrastichus giffardianus Silvestri. |
| | | Ceratitis punctata (Wiedemann) | Conopharyngia longiflora<br>Chrysophyllum pruniforme. | Hedylus giffardii Silvestri.<br>Diachasma fullawayi Silvestri.<br>Opius perproximus Silvestri.<br>Tetrastichus giffardianus Silvestri. |
| | | Dacus brevistylus Bezzi | Momordica charantia | - |
| | | Dacus punctatifrons Karsch | Passiflora foetida | Tetrastichus giffardianus Silvestri. |
| | | Dacus sp. nr. punctatifrons Karsch | Momordica charantia | - |
| | | Dacus sp. | cucumber | Opius sp. |
| | | Tridacus sp. nr. pectoralis (Walker) | Adenia lobata<br>Luffa cylindrica. | Opius sp. |
| | | Trirhithrum coffeae Bezzi | Coffea liberica | Opius sp. |
| | | Unidentified Tephritid | Cola nitida<br>cacao. | - |
| Liberia | IV-6. | - | - | |

| | | | | |
|---|---|---|---|---|
| Ivory Coast | IV-10 to IV-11. | - | - | - |
| Gold Coast | IV-4 and VI-14 to VI-15. | Ceratitis capitata (Wiedemann)[3/] | - | - |
| | | Ceratitis punctata (Wiedemann)[3/] | - | - |
| Nigeria | IV-17 to V-17. | Ceratitis anonae Graham[3/] | Gliricidia maculata | - |
| | | Ceratitis capitata (Wiedemann)[3/] | Gliricidia maculata | - |
| | | Ceratitis sp. nr. cosyra (Walker)[3/] | Gliricidia maculata | - |
| | | Ceratitis punctata (Wiedemann) | Landolphia sp.<br>Napoleona vogelii (?). | Hedylus (?) sp.<br>Opius sp. |
| | | Ceratitis tritea (Walker) | Conopharyngia penduliflora | - |
| | | Conradtina acroleuca (Wiedemann) | Napoleona vogelii (?) | Hedylus (?) sp. |
| | | Dacus brevistylus Bezzi | Momordica charantia (?) | Biosteres caudatus Szepligeti.<br>Hedylus (?) sp.<br>Opius sp. |
| | | Dacus ciliatus Loew[3/] | Gliricidia maculata | - |

Table 2. Continued
Summary of fruit flies and parasites[1] collected by R.H. Van Zwaluwenburg and J.M. McGough in West Africa during November 1935 to July 1936 (extracted from Van Zwaluwenburg 1936)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2] |
|---|---|---|---|---|
| Nigeria (Con.) | | Dacus rufus Bezzi[3] | Sterculia sp. | - |
| | | Dacus vertebratus Bezzi[3] | Gliricidia maculata | - |
| | | Tridacus pectoralis (Walker) | Adenia sp. (?) | - |
| French Cameroons | V-20 to VI-20 & VI-24 to VIII-23. | Bistrispinaria fortis (Speiser)[3] | - | - |
| | | Carpophthoromyia n. sp[3] | - | - |
| | | Ceratitis anonae Graham | avocado<br>Cola sp.<br>Conopharyngia spp.<br>Myrianthus arboreus. | Biosteres caudatus Szepligeti.<br>Hedylus (?) sp.<br>Tetrastichus giffardianus Silvestri.<br>hyperparasite (?). |
| | | Ceratitis cosyra (Walker)[3] | - | - |
| | | Ceratitis sp. nr. cosyra (Walker)[3] | - | - |
| | | Ceratitis punctata (Wiedemann) | Conopharyngia spp. | Biosteres caudatus Szepligeti.<br>Hedylus (?) sp.<br>Tetrastichus giffardianus Silvestri. |
| | | Ceratitis spp. | 'abam'<br>Cola digitata<br>Cola sp. (brown)<br>Cola sp. (green)<br>Conopharyngia sp.<br>Cuttifaera sp.<br>egg plant. | Biosteres sp.<br>'black parasites'.[4]<br>Hedylus sp.<br>Opius (?) sp.<br>'red parasites'.[4]<br>Tetrastichus sp. |

| | | | | |
|---|---|---|---|---|
| French Cameroons (Con.) | | Ceratitis sp. | Emilis-Marcela sp.<br>Myrianthus sp. | |
| | | Dacus sp. | eggplant<br>gourd<br>squash | Biosteres sp.<br>Hedylus (?) sp.<br>Opius sp. |
| | | Tridacus humeralis (Bezzi) | ? | Biosteres caudatus Szepligeti.<br>Opius sp. |
| Angola | VI-26 to VI-28. | - | - | - |
| Congo | VII-2 to VII-6. | Dacus n. sp. (nr. chrysomphalus) | Momordica sp. | - |

1/ Scientific names listed are those used by reporting scientist and may not be the most current or accepted binomials available.
2/ Listed parasites may not have been recovered from all listed host fruit.
3/ Captured in a sweep net or observed; not reared from host fruit.
4/ McGough refers to some parasites collected as 'red' or 'black' parasites but was unable to identify the species further.

Table 3.
Summary of fruit flies and parasites[1] collected by F.A. Bianchi and N.H. Krauss in East Africa during November 1935 to June 1936 (extracted from Bianchi and Krauss 1936)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2/] |
|---|---|---|---|---|
| Tanganyika | XI-14 to VI-13. | Ceratitis capitata (Wiedemann) | strawberry guava | - |
| | | Ceratitis colae Silvestri | conion guava<br>Drypetes bettiscombei<br>guava<br>Myrianthus arboreus<br>oranges<br>peaches<br>Sersalisia usumbarensis<br>strawberry guava. | Opius giffardii (Silvestri).<br>Opius perproximus Silvestri.<br>Tetrastichus dacicida Silvestri. |
| | | Ceratitis cosyra (Walker) | Cordyla africana | Opius perproximus Silvestri. |
| | | Ceratitis punctata (Wiedemann) | Sersalisia usumbarensis | Opius perproximus Silvestri.<br>Tetrastichus dacicida Silvestri. |
| | | Ceratitis rubivora Coquillett | blackberries<br>Myrianthus arboreus<br>peaches. | - |
| | | Dacus eclipsis (Bezzi) | Peponium sp. | - |
| | | Dacus sp. | Cucurbitaceae | - |
| | | Tridacus humeralis (Bezzi) | Cucurbitaceae | Opius sp.<br>Tetrastichus giffardii Silvestri. |
| | | Tridacus pectoralis (Walker) | Dioscorea macrura<br>Luffa sp.<br>Peponium sp. | - |
| | | Tridacus punctatifrons (Karsch) | Luffa sp.<br>Peponium sp. | - |

| | | | | |
|---|---|---|---|---|
| Tanganyika (Con.) | | Tridacus vertebratus (Bezzi) | Coccinea sp. | - |
| | | - | apples<br>apricots<br>citrus<br>Coccinia engleri<br>coffee<br>kueme nut<br>loquats<br>mango<br>oranges<br>Peponium usumbarensis<br>pepper<br>plums<br>quince<br>rose apple<br>Terminalia cattapa. | - |
| Zanzibar | XII-3 to XII-12 & XII-18 to I-5. | Ceratitis capitata (Wiedemann) | guava | - |
| | | Ceratitis colae Silvestri | guava | - |
| | | Ceratitis n. sp. | Psychotria sp. | - |
| | | Dacus brevistylus Bezzi | cucumber<br>Luffa aegyptica<br>Momordica charantia<br>pumpkin. | - |
| | | Tridacus pectoralis (Walker) | cucumber<br>Luffa aegyptica<br>Momordica charantia<br>pumpkin. | - |

Table 3. Continued
Summary of fruit flies and parasites[1] collected by F.A. Bianchi and N.H. Krauss in East Africa during November 1935 to June 1936 (extracted from Bianchi and Krauss 1936)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2/] |
|---|---|---|---|---|
| Zanzibar (Con.) | | Dacus sp. | cucumber | - |
| | | Tephritidae (unknown species) | cucumber | Dirhinus n. sp. |
| | | | Momordica charantia | Opius perproximus Silvestri. |
| | | | Psychotria sp. | Opius n. sp. |
| | | | pumpkin | Spalangia afra Silvestri. |
| | | - | Achras sapota | - |
| | | | avocado | |
| | | | citrus | |
| | | | duriano | |
| | | | mango | |
| | | | mangosteen | |
| | | | mulberries | |
| | | | papaya | |
| | | | pomegranate | |
| | | | rose apple | |
| | | | Spondias sp. | |
| | | | strawberry guava | |
| | | | tropical almond | |
| Kenya | IV-7 to VI-23. | Ceratitis bremii Guerin-Meneville | Acokenthera longiflora | Opius humilis Silvestri. |
| | | | Acokenthera sp. | Opius perproximus Silvestri. |
| | | | | Tetrastichus giffardianus Silvestri. |
| | | Ceratitis capitata (Wiedemann) | Acokenthera longiflora | Halticoptera sp. (?) |
| | | | Bruces antidysenterica | Opius fullawayi (Silvestri). |
| | | | Berberis holstii | Opius giffardii (Silvestri). |
| | | | coffee | Opius humilis Silvestri. |
| | | | Doryalis caffra | Opius perproximus Silvestri. |
| | | | loquat | Opius sp. |
| | | | strawberry guava | Tetrastichus giffardianus Silvestri. |
| | | | Tecles trichocarpa | |

| | | | |
|---|---|---|---|
| Kenya (Con.) | Ceratitis capitata | Tacsonia sp. | |
| | | Vanqueria sp. | |
| | Ceratitis colae Silvestri | coffee | Halticoptera sp. (?) |
| | | common guava | Opius fullawayi (Silvestri). |
| | | Doryalis caffra | Opius sp. |
| | | Himalayan blackberry | |
| | | loquat | |
| | | oranges | |
| | | peaches | |
| | | Podocarpus gracilior | |
| | | Rawosani usumbarensis | |
| | Ceratitis cosyra (Walker) | Acokenthera longiflora | Opius perproximus Silvestri. |
| | | Warburgia ugandensis | |
| | Ceratitis nigra Graham | Strichnos sp. | Microbracon celer (Szepligeti). |
| | | | Opius fullawayi (Silvestri). |
| | | | Opius perproximus Silvestri. |
| | | | Opius sp. |
| | | | Tetrastichus giffardianus Silvestri. |
| | | | Tetrastichus n. sp. |
| | Ceratitis rubivora Coquillett | Olea hochstetteri | Opius sp. |
| | | coffee | parasite spp. |
| | | cucurbits | |
| | | Deinbellia sp. | |
| | | blackberry | |
| | | Himalayan blackberry | |
| | | Melothria sp. | |
| | | Passiflora sp. | |
| | | Piper sp. | |
| | | peaches | |

Table 3. Continued
Summary of fruit flies and parasites[1] collected by F.A. Bianchi and N.H. Krauss in East Africa during November 1935 to June 1936 (extracted from Bianchi and Krauss 1936)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2/] |
|---|---|---|---|---|
| Kenya (Con.) | | Ceratitis rubivora | Pygeum africanum | |
| | | | Rawosani usumbarensis | |
| | | | Rubus sp. | |
| | | | Todalia assiatica (?) | |
| | | Ceratitis n. sp. | Bruces antidysenterica | Opius fullawayi (Silvestri). |
| | | | Solanum indicum (?) | Opius sp. |
| | | | Solanum naumanni | Tetrastichus oxyurus Silvestri. |
| | | Dacus eclipsis (Bezzi) | Peponium sp. | - |
| | | Tridacus humeralis (Bezzi) | cucurbits | Opius sp. |
| | | | | Tetrastichus giffardii Silvestri. |
| | | Tridacus pectoralis (Walker) | Peponium sp. | - |
| | | Tridacus punctatifrons (Karsch) | Peponium sp. | - |
| | | | Momordica sp. | - |
| | | Tridacus n. sp. | Duranta plumieri | Opius fullawayi (Silvestri). |
| | | | Melothria n. sp. | Opius perproximus Silvestri. |
| | | Tephritidae | Cissus nanaquensis | - |
| | | - | Allophyllus sp. | - |
| | | | Anona muricata | |
| | | | apple | |
| | | | asparagus | |
| | | | Cestrum aurantiacum | |
| | | | Cissanpelo parreria | |
| | | | Cissus mananquensis | |
| | | | Clerodendron myricoidea | |
| | | | Cotoneaster pennosa | |
| | | | Croton megalocarpon | |

| | | | |
|---|---|---|---|
| Kenya (Con.) | - | cucumber | - |
| | | custard apple | |
| | | dates | |
| | | Doryalis abyssinica | |
| | | Doryalis macrocalyx | |
| | | Dracaena fragrans | |
| | | Elaeodendron sp. | |
| | | Englerodaphne sp. | |
| | | Eugenia australis | |
| | | Feifoa sellowiana | |
| | | Ficus hockstetteri | |
| | | fig | |
| | | Ficus mallatocarpa | |
| | | Gardenia urcelliformis | |
| | | Grewia sp. | |
| | | Kigelia moosa | |
| | | Melia azedarach | |
| | | Melothria sp. | |
| | | Ochna sp. | |
| | | Olea chrysophyllia | |
| | | Olenia usumbarensis | |
| | | Peponia cucullata | |
| | | Phyllanthus discoides | |
| | | Phytolacoa dioica | |
| | | Pittosporum sp. | |
| | | plum | |
| | | Podocarpus milanjianus | |
| | | Prunus pudum | |
| | | Psychotria nairobensis | |
| | | Randia sp. | |
| | | Solanum auriculifera | |
| | | Solanum campylacanthum | |
| | | tangarine | |

Table 3. Continued
Summary of fruit flies and parasites[1] collected by F.A. Bianchi and N.H. Krauss in East Africa during November 1935 to June 1936 (extracted from Bianchi and Krauss 1936)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2] |
|---|---|---|---|---|
| Kenya (Con.) | | - | Tecles viridis<br>Vitex kenieasis<br>Xymalos monospora. | - |
| Uganda | IV-20 to VI-1. | Ceratitis colae Silvestri | Chrysophyllum albidum<br>common guava<br>Eugenia jambos<br>Myrianthus arboreus. | Ganaspis sp.<br>Opius n. sp. |
| | | Ceratitis rubivora Coquillett | avocado<br>common guava<br>Myrianthus arboreus. | - |
| | | Ceratitis n. sp. | Capparis erythrocarpa<br>Solanum naumanni. | Opius fullawayi (Silvestri).<br>Tetrastichus oxyurus (?) Silvestri. |
| | | Themarictera laticeps (Loew) | Capparis erythrocarpa | - |
| | | Tridacus pectoralis (Walker) | Vitex sp. | - |
| | | Tridacus punctatifrons (Karsch) | Chrysophyllum albidum | Ganaspis sp.<br>Opius n. sp. |
| | | tephritid larvae | Kimenia americana | - |
| | | - | Balanites aegyptiaca<br>Butyrospermum niloticum<br>Carissa edulis<br>Ficus verruculosa<br>Maesopsis eminii<br>Mimusops sp.<br>Sclerocaria birrea | - |

1/ Scientific names listed are those used by reported scientists and may not be the most current or accepted binomials available.
2/ Listed parasites may not have been recovered from all listed host fruit.

Table 4.
Summary of fruit flies and parasites[1] collected by F.C. Hadden in southeast Asia during December 1935 to June 1936 (extracted from Hadden 1936)

| Country | Collecting period | Host fruit fly | Host fruit | Parasites recovered[2/] |
|---|---|---|---|---|
| Malaya | XII-28 to IV-6. | Chaetodacus ferrugineus (Fabricius) | Averrhoa carambola<br>citrus<br>Eugenia uniflora<br>guava<br>chilli<br>Artocarpus integrifolia. | Opius fletcheri (?) Silvestri.<br>Opius persulcatus (Silvestri).<br>Spalangia sp.<br>Opius longicaudatus (Ashmead).<br>Pachycrepoideus sp.<br>Melittobia indicum (Silvestri). |
| | | Chaetodacus cucurbitae (Coquillett) | Tricosanthes anguis<br>cucumber<br>Momordica charantia<br>Luffa acutangula. | Opius fletcheri Silvestri. |
| | | Chaetodacus umbrosus (Fabricius) | Artocarpus integrifolia | - |
| | | Chaetodacus caudatus (Fabricius) | cucurbits | - |
| | | Chaetodacus dorsalis (Hendel) | citrus | - |
| Ceylon | IV-13 to V-9. | Chaetodacus ferrugineus (Fabricius) | mango | Opius fletcheri Silvestri.<br>Opius longicaudatus (Ashmead). |
| | | Chaetodacus garciniae (?) (Bezzi) | Garcinia tinctoria<br>Tricosanthes anguis. | Opius longicaudatus (Ashmead).<br>Opius fletcheri Silvestri. |
| India | V-11 to VI-24. | Chaetodacus cucurbitae (Coquillett) | cucumbers | Dirhinus auratus Ashmead. |
| | | Chaetodacus ferrugineus (Fabricius) | Solanum sp. | Opius persulcatus (Silvestri). |

1/ Scientific names listed are those used by recording scientists and may not be most current or accepted bionomials available.
2/ Listed parasites may not have been recovered from all listed host fruit.

Table 5.
Fruit fly parasites shipped to the Hawaiian Islands during the 1947-52 biological control on Dacus dorsalis and their status in Hawaii (extracted from Bess et al. 1961; Clausen et al. 1965)[1]

| Family and parasite species[2] | Origin[3] | | Reported status in Hawaii[4] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly | Released | Recovered | Established |
| BRACONIDAE | | | | | |
| Bracon celer Szepligeti | Kenya | Ceratitis capitata (Wiedemann) | - | - | - |
| Bracon fletcheri Silvester | India | Carpomyia vesuviana A. Costa | + | - | - |
| Cratospila sp. | India | Dacus nubilus Hendel | - | - | - |
| Opius africanus Szepligeti | Kenya | Ceratitis capitata (Wiedemann)<br>Pterandrus rosa (Karsch)<br>Trirhithrum coffeae Bezzi. | - | - | - |
| Opius anastrephae (Viereck) | Brazil | Anastrepha mombinpraeoptans Sein<br>Anestrepha serpentina (Wiedemann) | + | - | - |
| Opius angaleti Fullaway | N. Borneo | Callantra smieroides Walker<br>Dacus cucurbitae Coquillett (?)<br>Dacus hageni de Meijere. | + | - | - |
| Opius arisanus Sonan | China (?)<br>Thailand<br>Formosa. | Dacus dorsalis Hendel | - | - | - |
| Opius bevisi Brues (?) | Kenya | Trirhithrum queritum Munro | + | - | - |
| Opius bianchii Fullaway | Thailand | (?) | - | - | - |
| Opius carpomyiae (Silvestri) | India | Carpomyia vesuviana A. Costa | - | - | - |
| Opius caudatus (Szepligeti) | Belgian-Congo<br>Kenya. | Dacus bivittatus (Bigot)<br>Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett | - | - | - |

| | | | | | |
|---|---|---|---|---|---|
| Opius caudatus (Szepligeti) (Con.) | | Pardalaspis ditissima Munro<br>Pterandrus anonae (Graham)<br>Trirhithrum coffeae Bezzi. | | | |
| Opius cereus Gahan | Brazil | Anastrepha mombinpraeoptans Sein<br>Anastrepha serpentina (Wiedemann) | + | - | - |
| Opius compensans (Silvestri) | India | Dacus dorsalis Hendel<br>Dacus incisus Walker (?)<br>Dacus latifrons (Hendel)<br>Dacus nubilus Hendel | + | + | - |
| Opius concolor Szepligeti | Belgian Congo<br>Kenya | Dacus oleae (Gmelin)<br>Pterandrus anonae (Graham)<br>Trirhithrum coffeae Bezzi | - | - | - |
| Opius crawfordi Viereck | Mexico | Anastrepha ludeus (Loew) | - | - | - |
| Opius deeralensis Fullaway | Australia<br>New Britian | Dacus barringtoniae (Tryon)<br>Dacus endiandrae (Perkins & May)<br>Dacus fagraeus (Tryon)<br>Dacus frauenfeldi Schiner<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus laticaudus Hardy<br>Dacus murrayi (Perkins)<br>Dacus musae (Tryon)<br>Dacus pallidus (Perkins & May)<br>Dacus tryoni (Froggatt) | + | - | - |
| Opius desideratus (Bridwell) | Belgian Congo<br>Cameroon | Pardalespis ditissima Munro<br>Pterandrus anonae (Graham)<br>Trirhithrum coffeae Bezzi | - | - | - |

Table 5. Continued
Fruit fly parasites shipped to the Hawaiian Islands during the 1947-52 biological control on Dacus dorsalis and their status in Hawaii (extracted from Bess et al. 1961; Clausen et al. 1965)[1/]

| Family and parasite species[2/] | Origin[3/] | | Reported status in Hawaii[4/] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly | Released | Recovered | Established |
| Opius fijiensis Fullaway | Australia<br>Fiji<br>New Britain<br>New Caledonia | Dacus barringtoniae (Tryon)<br>Dacus curvipennis (Froggat)<br>Dacus endriandrae (Perkins & May)<br>Dacus sp. near facialis Coquillett<br>Dacus fagraeus (Tryon)<br>Dacus frauenfeldi Schiner<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus laticaudus Hardy<br>Dacus murrayi (Perkins)<br>Dacus musae (Tryon)<br>Dacus pallidus (Perkins & May)<br>Dacus passiflorae (Froggatt)<br>Dacus psidii (Froggatt)<br>Dacus tryoni (Froggatt) | + | - | - |
| Opius fletcheri Silvestri | Ceylon<br>India<br>Malaya<br>Phillipine Is. | Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett<br>Dacus hageni de Meijere<br>Dacus limbiferus (Bezzi)<br>Dacus nubilus Hendel | + | + | + |
| Opius formosanus (Fullaway) | Formosa | Dacus dorsalis Hendel | + | + | + |
| Opius froggatti Fullaway | Australia<br>New Caledonia | Dacus kraussi Hardy<br>Dacus laticaudus Hardy<br>Dacus psidii (Froggatt)<br>Dacus tryoni (Froggatt) | - | - | - |
| Opius fullawayi (Silvestri) | Belgian Congo<br>Cameroon | Pterandrus anonae (Graham)<br>Trirhithrum coffeae Bezzi | - | - | - |

| | | | | | |
|---|---|---|---|---|---|
| Opius fuscipennis (Szepligeti) | Belgian Congo<br>Cameroon | Pardalaspis dittissima Munro<br>Pterandrus anonae (Graham)<br>Trirhirthrum coffeae Bezzi | - | - | - |
| Opius giffardii (Silvestri) | Belgian Congo<br>Kenya | Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew<br>Pardalaspis contramedia Munro<br>Pardalaspis ditissima Munro<br>Pterandrus anonae (Graham) | - | - | - |
| Opius hageni Fullaway | Fiji | Dacus passiflorae (Froggatt)<br>Dacus xanthodes (Brown) | - | - | - |
| Opius humilis Silvestri | South Africa | Ceratitis capitata (Wiedemann) | - | - | - |
| Opius incisi Silvestri | India<br>Malaya<br>N. Borneo<br>Philippine Is.<br>Thailand | Dacus ciliatus Loew (?)<br>Dacus cucurbitae Coquillett (?)<br>Dacus dorsalis Hendel<br>Dacus incisus Walker<br>Dacus nubilus Hendel | + | + | + |
| Opius kraussi Fullaway | Australia | Dacus barringtoniae (Tryon)<br>Dacus cacuminatus (Hering)<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus murrayi (Perkins & May)<br>Dacus pallidus (Perkins & May)<br>Dacus tryoni (Froggatt) | + | + | - |
| Opius longicaudatus (Ashmead) | India<br>New Britain<br>N. Borneo<br>Philippine Is.<br>Saipan | Dacus ciliatus Loew (?)<br>Dacus cucurbitae Coquillett<br>Dacus dorsalis Hendel<br>Dacus frauenfeldi Schiner<br>Dacus limbiferus (Bezzi) | - | - | - |

Table 5. Continued
Fruit fly parasites shipped to the Hawaiian Islands during the 1947-52 biological control on Dacus dorsalis and their status in Hawaii (extracted from Bess et al. 1961; Clausen et al. 1965)[1/]

| Family and parasite species[2/] | Origin[3/] | | Reported status in Hawaii[4/] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly | Released | Recovered | Established |
| Opius longicaudatus Con. | | Dacus nubilus Hendel<br>Dacus ochrosiae Malloch<br>Dacus zonatus (Saunders) | | | |
| O. l. var. chocki Fullaway | Philippine Is. | Dacus dorsalis Hendel<br>Dacus limbiferus (Bezzi) | + | - | - |
| O. l. var. malaiensis Fullaway | Malaya | Dacus dorsalis Hendel | + | + | + |
| O. l. var. novocaledonicus Fullaway | New Caledonia | Dacus curvipennis (Froggatt)<br>Dacus sp. nr. facilais Coquillett<br>Dacus psidii (Froggatt) | + | + | + |
| O. l. var. taiensis Fullaway | Thailand | Carpomyia vesuviana A. Costa<br>Dacus dorsalis Hendel<br>Dacus latifrons (Hendel) | + | + | + |
| Opius lounsburyi Silvestri (?) | Kenya | Dacus oleae (Gmelin) | - | - | - |
| Opius makii Sonan | Formosa<br>Java<br>Philippine Is.<br>Thailand | Dacus dorsalis (Hendel)<br>Dacus nubilus Hendel | + | - | - |
| Opius manii Fullaway | India | Dacus dorsalis Hendel | - | - | - |
| Opius oophilus Fullaway | Java<br>Fiji<br>Formosa<br>India<br>Malaya<br>N. Borneo<br>Philippine Is.<br>Thailand | Carpomyia vesuviana A. Costa<br>Dacus dorsalis Hendel<br>Dacus incisus Walker (?)<br>Dacus latifrons (Hendel)<br>Dacus passiflorae (Froggatt) | + | + | + |

| | | | | | |
|---|---|---|---|---|---|
| CHALCIDIDAE | | | | | |
| Dirhinus giffardii Silvestri | Australia<br>India<br>Kenya | Carpomyuia vesuviana A. Costa<br>Dacus bivittatus cucumarius Sack<br>Dacus cacuminatus (Hering)<br>Dacus ciliatus Loew<br>Dacus correctus (Bezzi)<br>Dacus cucurbitae Coquillett<br>Dacus dorsalis Hendel<br>Dacus endiandrae (Perkins & May)<br>Dacus incisus Walker<br>Dacus kraussi Hardy<br>Dacus laticaudus Hardy<br>Dacus latifrons (Hendel)<br>Dacus nubilus Hendel<br>Dacus zonatus (Sanders) | + | - | - |
| Dirhinus luzonensis Rohwer | India | Carpomyia vesuviana A. Costa<br>Dacus ciliatus Loew<br>Dacus correctus (Bezzi)<br>Dacus cucurbitae Coquillett<br>Dacus dorsalis Hendel<br>Dacus incisus Walker<br>Dacus latifrons (Hendel)<br>Dacus nubilus Hendel<br>Dacus zonatus (Saunders) | - | - | - |
| CYNIPIDAE | | | | | |
| Cothonaspis sp. | India | Dacus dorsalis Hendel<br>Dacus incisus Walker (?) | - | - | - |
| Pilinothrix sp. | Malaya | Dacus dorsalis Hendel<br>Dacus incisus Walker (?)<br>Dacus umbrosus Fabricius | - | - | - |

Table 5. Continued
Fruit fly parasites shipped to the Hawaiian Islands during the 1947-52 biological control on Dacus dorsalis and their status in Hawaii (extracted from Bess et al. 1961; Clausen et al. 1965)[1/]

| Family and parasite species[2/] | Origin[3/] | | Reported status in Hawaii[4/] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly | Released | Recovered | Established |
| Opius perkinsi Fullaway | Australia | Dacus cacuminatus (Hering)<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus laticaudus Hardy<br>Dacus tryoni (Froggatt) | - | - | - |
| Opius perproximus Silvestri | Kenya | Pterandrus rosa (Karsch) | - | - | - |
| Opius persulcatus (Silvestri) | India | Dacus dorsalis Hendel<br>Dacus incisus Walker (?)<br>Dacus latifrons (Hendel)<br>Dacus zonatus (Saunders) (?) | - | - | - |
| Opius phaeostigma Wilkinson | Belgian Congo<br>Cameroon<br>Kenya | Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew<br>Carpophthoromyia dimidiata Bezzi<br>Pardalaspis contramedia Munro<br>Pardalaspis ditissima Munro<br>Trirhithrum queritum Munro | + | - | - |
| Opius skinneri Fullaway | Philippine Is. | Dacus limbiferus (Bezzi)<br>Dacus pedestris (Bezzi) | + | - | - |
| Opius vandenboschi Fullaway | Formosa<br>India<br>Java<br>Malaya<br>N. Borneo<br>Philippine Is.<br>Thailand | Dacus cucurbitae Coquillett (?)<br>Callantra smieroides Walker<br>Dacus dorsalis Hendel<br>Dacus hageni de Meijere | + | + | + |
| Opius watersi Fullaway | Ceylon<br>India | Dacus cucurbitae Coquillett<br>Dacus ciliatus Loew<br>Dacus nubilus Hendel | + | + | - |

| | | | | | |
|---|---|---|---|---|---|
| Pseudeucoila sp. | India<br>Malaya | Dacus dorsalis Hendel<br>Dacus umbrosus Fabricius | - | - | - |
| Trybliographa daci Weld | Australia<br>India<br>Malaya<br>N. Borneo | Dacus barringtoniae (Tryon)<br>Dacus cucurbitae Coquillett (?)<br>Dacus dorsalis Hendel<br>Dacus incisus Walker (?)<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus tryoni (Froggatt)<br>Dacus umbrosus Fabricius | + | - | - |
| DIAPRIIDAE | | | | | |
| Psilus magnificus (Nixon) | Kenya | Pardalaspis contramedia Munro | - | - | - |
| Psilus silvestrii Kieffer | Kenya | Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew | - | - | - |
| Trichopria sp. | Belgian Congo<br>India | Dacus ciliatus Loew (?)<br>Dacus cucurbitae Coquillett (?)<br>Dacus dorsalis Hendel<br>Dacus incisus Walker (?)<br>Dacus nubilus Hendel<br>Pterandrus anonae (Graham) | - | - | - |
| EULOPHIDAE | | | | | |
| Aceratoneuromyia indica (Silvestri) | Ceylon<br>Fiji<br>India<br>Java<br>Malaya<br>N. Borneo<br>Philippine Is. | Dacus cucurbitae Coquillett (?)<br>Dacus dorsalis Hendel<br>Dacus incisus Walker (?)<br>Dacus nubilus Hendel<br>Dacus passiflorae (Froggatt)<br>Dacus xanthodes (Brown) (?) | + | - | - |

Table 5. Continued
Fruit fly parasites shipped to the Hawaiian Islands during the 1947-52 biological control on Dacus dorsalis and their status in Hawaii (extracted from Bess et al. 1961; Clausen et al. 1965)[1/]

| Family and parasite species[2/] | Origin[3/] | | Reported status in Hawaii[4/] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly | Released | Recovered | Established |
| Tetrastichus dacicida Silvestri | Belgian Congo<br>Java<br>Kenya | Carpophthoromyia dimidiata Bezzi<br>Ceratitus capitata (Wiedemann)<br>Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett<br>Pardalaspis contramedia Munro<br>Pardalaspis ditissima Munro<br>Pterandrus anonae (Graham)<br>Pterandrus rosa (Karsch)<br>Trirhithrum queritum Munro | + | + | - |
| Tetrastichus giffardianus (Silvestri) | Kenya<br>South Africa | Carpophthoromyia dimidiata Bezzi<br>Ceratitis capitata (Wiedemann)<br>Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett<br>Pardalaspis contramedia Munro<br>Pardalaspis sp.<br>Pterandrus rosa (Karsch)<br>Trirhithrum queritum Munro | + | + | + |
| Tetrastichus giffardii Silvestri | Cameroon<br>Kenya<br>India | Carpophthoromyia dimidiata Bezzi<br>Ceratitis capitata (Wiedemann)<br>Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett<br>Pardalaspis contramedia Munro<br>Pardalaspis sp.<br>Pterandrus anonae (Graham)<br>Pterandrus rosa (Karsch)<br>Trirhithrum queritum Munro | - | - | - |
| PTEROMALIDAE | | | | | |
| Halticoptera daci Silvestri (?) | Australia | Dacus tryoni (Froggatt) | - | - | - |
| Pachycrepoideus vindemmiae (Rondani) | Australia<br>Belgian Congo<br>China<br>Formosa | Carpomyia vesuviana A. Costa<br>Dacus cacuminatus (Hering)<br>Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett | - | - | - |

| | | | | |
|---|---|---|---|---|
| Pachycrepoideus vindemmiae (Con.) | India | Dacus dorsalis Hendel | | |
| | Kenya | Dacus endiandrae (Perkins & May) | | |
| | Malaya | Dacus latifrons Hardy | | |
| | N. Borneo | Dacus latifrons (Hendel) | | |
| | Philippine Is. | Dacus limbiferus (Bezzi) | | |
| | Thailand | Dacus musae (Tryon) | | |
| | | Dacus nubilus Hendel | | |
| | | Dacus tryoni (Froggatt) | | |
| | | Dacus zonatus (Saunders) | | |
| | | Pardalaspis contramedia Munro | | |
| | | Pardalaspis ditissima Munro | | |
| | | Rhagoletis sp. (?) | | |
| Spalangia afra Silvestri | Australia | Carpomyia vesuviana A. Costa | - | - |
| | Belgian Congo | Dacus bivittatus cucumarius Sack | | |
| | Kenya | Dacus cacuminatus (Hering) | | |
| | India | Dacus ciliatus Loew | | |
| | | Dacus cucurbitae Coquillett | | |
| | | Dacus dorsalis Hendel | | |
| | | Dacus endiandrae (Perkins & May) | | |
| | | Dacus incisus Walker (?) | | |
| | | Dacus jarvisi (Tryon) | | |
| | | Dacus kraussi Hardy | | |
| | | Dacus latifrons (Hendel) | | |
| | | Dacus nubilus Hendel | | |
| | | Dacus tryoni (Froggatt) | | |
| | | Dacus zonatus (Saunders) | | |
| | | Pardalaspis ditissima Munro | | |
| | | Pterandrus anonae (Graham) | | |
| Spalangia endius Walker | Australia | Carpomyia vesuviana A. Costa | + | - |
| | Fiji | Dacus cacuminatus (Hering) | | |
| | India | Dacus ciliatus Loew | | |
| | Malaya | Dacus cucurbitae Coquillett | | |
| | New Caledonia | Dacus curvipennis (Froggatt) | | |
| | | Dacus dorsalis Hendel | | |
| | | Dacus endiandrae (Perkins & May) | | |

Table 5. Continued
Fruit fly parasites shipped to the Hawaiian Islands during the 1947-52 biological control on Dacus dorsalis and their status in Hawaii (extracted from Bess et al. 1961; Clausen et al. 1965)[1/]

| Family and parasite species[2/] | Origin[3/] | | Reported status in Hawaii[4/] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly | Released | Recovered | Established |
| Spalangia endius (Con.) | | Dacus sp. nr. facialis Coquillett<br>Dacus hageni de Meijere<br>Dacus incisus Walker (?)<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus latifrons (Hendel)<br>Dacus nubilus Hendel<br>Dacus passiflorae (Froggatt)<br>Dacus psidii (Froggatt)<br>Dacus tryoni (Froggatt)<br>Dacus zonatus (Saunders) | | | |
| Spalangia grotiusi Girault | Australia<br>India | Dacus cacuminatus (Hering)<br>Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett<br>Dacus dorsalis Hendel<br>Dacus endiandrae (Perkins & May)<br>Dacus incisus Walker (?)<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus latifrons (Hendel)<br>Dacus tryoni (Froggatt)<br>Dacus zonatus (Saunders) | - | - | - |
| Spalangia sp. nr. simplex Perkins | Malaya | Dacus cucurbitae Coquillett<br>Dacus dorsalis Hendel<br>Dacus hageni de Meijere | - | - | - |
| ENCYRTIDAE | | | | | |
| Tachinaephagus spp. | Belgian Congo<br>Formosa<br>India<br>Malaya | Dacus cucurbitae Coquillett<br>Dacus dorsalis Hendel<br>Dacus hageni de Meijere<br>Dacus latifrons (Hendel) | - | - | - |

| | | | |
|---|---|---|---|
| Tachinaephagus spp. (Con.) | Thailand | Dacus nubilus Hendel<br>Dacus umbrosus Fabricius<br>Pterandrus anonae (Graham) | |

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[1]Scientific names and place names are those used by reporting scientist and may not be the most current or accepted names.
[2]Parasites listed are primarily those with proper binomials; generic representations are only for those taxa which are not otherwise presented in the table.
[3]Fruit flies listed are not necessarily from each listed geographic origin but were reported for at least one of the listed countries; because only pupal remains are available for host fly identification, some fly species listed as hosts may not in fact be hosts but were present as adult flies among the emerged parasites in a given shipment thus obscuring host relationships; (?) indicates Clausen et al. (1965) questioned veracity.
[4]+ indicates that the parasite species was released, recovered, or established in Hawaii; - indicates species was not released, recovered, or established.

Table 6.
Parasites collected during the 1947-52 Hawaiian Islands Oriental fruit fly project and which attacked C. capitata in the laboratory and/or in the field[1/]

| Family and parasite species | Origin | | Status in Hawaii[3/] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly[2/] | Re-leased | Recov-ered | Estab-lished |
| BRACONIDAE | | | | | |
| Opius angaleti Fullaway | Borneo | Dacus cucurbitae (?) Coquillett | Yes | No | No ? |
| Opius "caudatus" (Szepligeti) | Borneo<br>Congo | Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew<br>Pardalaspis ditissima Munro<br>Pterandrus anonae (Graham)<br>Trirhithrum coffeae Bezzi | No | No | No |
| Opius cereus Gahan | Brazil | Anastrepha mombinpraeoptans Sein<br>Anastrepha serpentina (Wiedemann) | Yes | No | No ? |
| Opius compensans (Silvestri) | India | Dacus dorsalis Hendel<br>Dacus incisus (?) Walker<br>Dacus latifrons (Hendel)<br>Dacus nubilus Hendel | Yes | Yes | ? |
| Opius concolor Szepligeti var. ? | Congo | Pterandrus anonae (Graham)<br>Trirhithrum coffeae Bezzi | No | No | No |
| Opius desideratus (Bridwell) | Cameroon | Pterandrus anonae (Graham) | No | No | No |
| Opius fletcheri Silvestri | Ceylon<br>India<br>Malaya | Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett<br>Dacus hageni Meijere | Yes | Yes | Yes |
| Opius formosanus (Fullaway) | Formosa | Dacus dorsalis Hendel | Yes | Yes | ? |
| Opius fuscipennis (Szepligeti) | Cameroon<br>Congo | Pardalaspis ditissima Munro<br>Pterandrus anonae (Graham)<br>Trirhithrum coffeae Bezzi | No | No | No |

| | | | | | |
|---|---|---|---|---|---|
| Opius giffardii (Silvestri) | Congo<br>Kenya | Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew<br>Pardalaspis contramedia Munro<br>Pardalaspis ditissima Munro<br>Pterandrus anonae (Graham) | No | No | No |
| Opius hageni Fullaway | Fiji | Dacus passiflorae Froggatt<br>Dacus xanthodes Braun | No | No | No |
| Opius incisi Silvestri | Borneo<br>India<br>Malaya<br>Philippines<br>Thailand | Dacus ciliatus (?) Loew<br>Dacus cucurbitae (?) Coquillett<br>Dacus dorsalis Hendel<br>Dacus incisus (?) Walker<br>Dacus nubilis Hendel | Yes | Yes | Yes |
| Opius kraussi Fullaway | Australia | Dacus barringtoniae (Tryon)<br>Dacus cacuminatus (Hering)<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus murrayi (Perkins)<br>Dacus pallidus (Perkins & May)<br>Dacus tryoni (Froggatt) | Yes | Yes | Yes |
| Opius longicaudatus (Ashmead) | Borneo<br>New Britain<br>Philippines<br>Saipan | Dacus ciliatus Loew<br>Dacus dorsalis Hendel<br>Dacus frauenfeldi Schiner<br>Dacus limbiferus (Bezzi)<br>Dacus zonatus (Saunders) | No | No | No |
| O. l. var. malaiensis Fullaway | Malaya | Dacus dorsalis Hendel | Yes | Yes | Yes |
| O. l. var. novocaledonicus Fullaway | New Caledonia | Dacus curvipennis Froggatt<br>Dacus sp. nr. facialis Coquillett | Yes | Yes | Yes |

Table 6. Continued
Parasites collected during the 1947-52 Hawaiian Islands Oriental fruit fly project and which attacked C. capitata in the laboratory and/or in the field[1/]

| Family and parasite species | Origin | | Status in Hawaii[3/] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly[2/] | Re-leased | Recov-ered | Estab-lished |
| O. l. var. novocaledonicus (Cont.) | | Dacus psidii (Froggatt) | | | |
| O. l. var. taiensis Fullaway | Thailand | Dacus dorsalis Hendel<br>Carpomya vesuviana Costa | Yes | Yes | Yes |
| Opius makii Sonan | Formosa<br>Java<br>Thailand | Dacus dorsalis Hendel | Yes | No | No ? |
| Opius manii Fullaway | India | Dacus dorsalis Hendel | No | No | No |
| Opius oophilus Fullaway | Fiji<br>India<br>Malaya<br>Philippines<br>Thailand | Dacus dorsalis Hendel<br>Dacus incisus (?) Walker<br>Dacus latifrons (Hendel)<br>Dacus passiflorae Froggatt | Yes | Yes | Yes |
| Opius persulcatus (Silvestri) | India | Dacus dorsalis Hendel<br>Dacus incisus (?) Walker<br>Dacus latifrons (Hendel)<br>Dacus zonatus (?) (Saunders) | No | No | No |
| Opius phaeostigma Wilkinson | Congo<br>Kenya | Dacus bivittatus cucumarius Sack<br>Dacus ciliatus Loew<br>Carpophthoromyia dimidiata Bezzi<br>Pardalaspis contramedia Munro<br>Pardalaspis ditissima Munro<br>Pterandrus anonae (Graham)<br>Trirhithrum queritum Munro | Yes | No | No ? |
| Opius watersi Fullaway | Ceylon | Dacus cucurbitae Coquillett | Yes | Yes | No ? |

| | | | | | |
|---|---|---|---|---|---|
| Opius vandenboschi Fullaway | Borneo<br>India<br>Java<br>Malaya<br>Philippines<br>Thailand | Dacus cucurbitae (?) Coquillett<br>Dacus dorsalis Hendel | Yes | Yes | Yes |
| CYNIPIDAE | | | | | |
| Trybliographa daci Weld | Borneo<br>Australia | Dacus cucurbitae (?) Coquillett<br>Dacus jarvisi (Tryon)<br>Dacus kraussi Hardy<br>Dacus tryoni (Froggatt) | Yes | No | No ? |
| PTEROMALIDAE | | | | | |
| Pachycrepoideus vindemiae (Rondani) | Borneo<br>Congo<br>Formosa<br>India<br>Malaya<br>Thailand | Carpomyia vesuviana Costa<br>Dacus cacuminatus (Hering)<br>Dacus ciliatus Loew<br>Dacus cucurbitae Coquillett<br>Dacus dorsalis Hendel<br>Dacus endiandrae (Perkins & May)<br>Dacus laticaudus Hardy<br>Dacus latifrons (Hendel)<br>Dacus musae (Tryon)<br>Dacus nubilis Hendel<br>Dacus tryoni (Froggatt)<br>Dacus zonatus (Saunders)<br>Pardalaspis contramedia Munro<br>Pterandrus ditissima Munro | No | No | No |
| EULOPHIDAE | | | | | |
| Aceratoneuromyia indicum (Silvestri) | Borneo<br>Ceylon<br>Fiji | Dacus cucurbitae (?) Coquillett<br>Dacus dorsalis Hendel<br>Dacus incisus (?) Walker | Yes | Yes | Yes |

Table 6. Continued
Parasites collected during the 1947-52 Hawaiian Islands Oriental fruit fly project and which attacked C. capitata in the laboratory and/or in the field[1/]

| Family and parasite species | Origin | | Status in Hawaii[3/] | | |
|---|---|---|---|---|---|
| | Geographic | Host fruit fly[2/] | Released | Recovered | Established |
| Aceratoneuromyia indicum (Cont.) | India | Dacus nubilus Hendel | | | |
| | Malaya | Dacus passiflorae (?) Froggatt | | | |
| | Philippines | Dacus xanthodes (?) Braun | | | |
| Tetrastichus dacidida Silvestri | Congo | Pardalaspis ditissima Munro<br>Pterandrus anonae (Graham) | Yes | Yes | ? |

1/ Information extracted from Clausen et al. (1965) and Bess et al. (1961); scientific names and place names are those used by reporting scientists and may not be the most curent or accepted names available.

2/ Fruit flies listed are not necessarily from each listed geographic origin, but were reported for at least one of the listed countries.

3/ Parasites listed as "No ?" were reported by Clausen et al. (1965) as not being established; ? denotes the possibility that a released parasite may be established at very low densities despite its not being recovered or reported as established.

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